

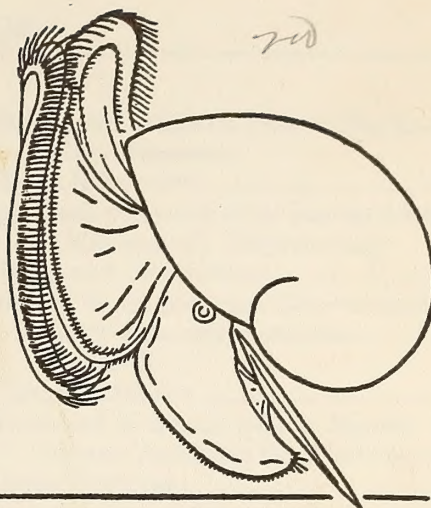




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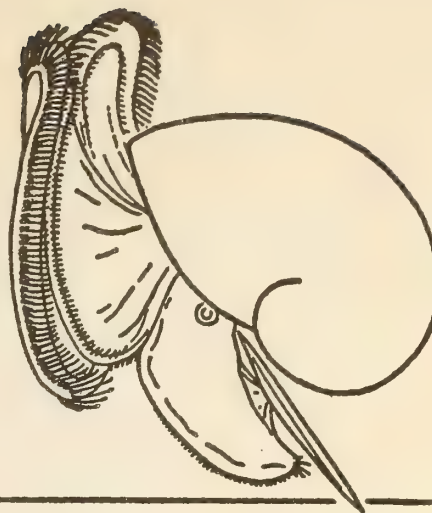
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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus*, (*Subgenus*)

New Taxa

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Reproductive Biology of *Colus stimpsoni*

(Prosobranchia : Buccinidae)

II. Spermiogenesis¹

BY

DAVID L. WEST²

(3 Plates)

INTRODUCTION

MOLLUSCAN SPERMATOOZA, like most sperm, are highly specialized for motility and the other activities involved in fertilization of the ova. RETZIUS (1906), in his splendid monograph, described and illustrated the male gametes for a number of different gastropods. His survey indicates that there is considerable heterogeneity in size and shape of gastropod spermatozoa. FRANZEN (1955) investigated a great variety of mollusks and concluded that the observed morphological modifications are related to the differences in the media into which the spermatozoa are discharged and fertilization occurs. He (FRANZEN, 1955, 1970) suggested that in those molluscan groups which have external fertilization, the spermatozoa are less morphologically specialized (primitive sperm type) than in those groups with internal fertilization (modified types of spermatozoa).

Most neogastropod spermatozoa, particularly those involved in fertilization, are thread-like in shape and are considered as a modified type which is associated with internal fertilization (FRANZEN, 1955, 1970; FAWCETT, 1970). Many investigators have contributed to the understanding of the structure, genesis, and functioning of subcellular components of molluscan spermatozoa (for more extensive literature, see TUZET, 1930; DUPOUY, 1964; ROOSEN-RUNGE, 1969; THOMPSON, 1973; ANDERSON & PERSONNE, 1970). However, many questions concerning these aspects of spermatozoa still remain.

An interesting phenomenon occurring in prosobranchs is sperm dimorphism; that is 2 or more morphologically distinct types of spermatozoa simultaneously produced by an individual male. Since VON SIEBOLD (1836) described this phenomenon, many workers have investigated the

genesis and function of these spermatozoa (PORTMANN, 1930; TUZET, 1930; DUPOUY, 1964; TOCHIMOTO, 1967; NISHIWAKI, 1964), and a variety of terms has been used for their designation. MEVES (1903) termed those spermatozoa which contain the normal complement of chromatin, "eupyrene"; those spermatozoa which have a smaller quantity of chromatin, "oligopyrene"; and those which have no chromatin, "apyrene." KUSCHAKEWITSCH (1913) later shortened the terminology to "typical" for the normal, eupyrene spermatozoa and "atypical" for all abnormal, oligopyrene and apyrene spermatozoa.

Atypical prosobranch spermatozoa exhibit various shapes and sizes, ranging from small worm-like forms to the giant, multiflagellated spermiozeugma. NISHIWAKI (1964) classified atypical spermatozoa into 8 morphological categories. TOCHIMOTO (1967) cytochemically examined a number of examples representing these categories and added one additional type of atypical spermatozoa, the "free cell" of the Littorinidae.

A few workers (ANKEL, 1924; PORTMANN, 1926, 1927, 1930, 1931; WOODWARD, 1940; BULNHEIM, 1962; REINKE, 1914) have dealt with the function of atypical spermatozoa, and some have suggested that they may serve a nurse-cell function (WOODWARD, *op. cit.*). Others (PORTMAN, *opp. cit.*; DUPOUY, 1964) have proposed that the atypical spermatozoa play a role in the determination of nutritive eggs (*i. e.*, those ova which are deposited in a single egg capsule but abort in early embryogenesis and serve as food for the developing young). However, not all prosobranchs that exhibit sperm dimorphism utilize nutritive eggs, nor do all those prosobranchs that utilize nutritive eggs exhibit sperm dimorphism (HYMAN, 1967; FRETTER & GRAHAM, 1962). PORTMANN (1931) suggested that in those species which do not exhibit a morphological sperm dimorphism but utilize nutritive eggs in the course of their development, for example *Thais lapillus* (Linnaeus, 1758), have a "physiological" sperm dimorphism. This dimorphism is a result of chromosome elimination in a portion of the gametes during meiosis (oligopyrene sperm)

¹ Contribution No. 58 from the Marine Science Institute, Northeastern University, Nahant, Massachusetts

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and fertilization of ova by these spermatozoa results in abortive embryos which then serve as a food source. STAIGER (1950, 1951) and THOMPSON (1973) indicate that atypical spermatozoa are incapable of participating in egg-penetration or amphimixis.

Members of the neogastropod genus *Colus* utilize nutritive eggs (THORSON, 1935, 1940; RADWIN & CHAMBERLIN, 1973; WEST, 1973) but little is known about the reproductive biology of this genus. The present study reports some ultrastructural and cytochemical findings on spermiogenesis in a species of *Colus* to further the knowledge of this genus and to add to the body of information concerning molluscan spermatozoa.

MATERIALS AND METHODS

Mature *Colus stimpsoni* (Mörch, 1867) were collected intertidally at Cobscook State Park, Edmunds, Maine, and at Eastport, Maine, and maintained in running sea water aquaria at the Marine Science Institute, Northeastern University, Nahant, Massachusetts. For light microscopy testes were excised from freshly opened, unrelaxed snails and fixed for 1-24 hours in the following: (a) Hollande-Bouin's; (b) Bouin's; (c) sea water Bouin's (WALKER & MACGREGOR, 1968); (d) buffered formalin (pH 7.4), or (e) buffered glutaraldehyde (pH 7.4). Following fixation, tissues were dehydrated through a graded series of ethanol or acetones and embedded in polyester wax (STEEDMAN, 1960). Sections were cut 4-6 μ m in thickness and stained with the following: (a) Heidenhain's azan, (b) Heidenhain's iron hematoxylin, (c) GABE's (1968) modification of Gomori's trichrome, (d) the Feulgen technique, or (e) the periodic acid-Schiff (PAS) technique (HUMASON, 1967). LEHMAN's (1965) polychrome was used for localizing various molecular groups.

Permanent sperm smears were prepared by diluting sperm from the seminal vesicle with sea water and placing a few drops of this suspension on glass slides. The slides were inverted over formalin vapors for 1-2 hours and subsequently washed briefly with distilled water. The Feulgen reaction (HUMASON, 1967) was used to localize the

sperm head, and Altmann's aniline-fuchsin technique (HUMASON, *op. cit.*) was employed to localize the middle piece. The PAS technique was used to determine the presence and distribution of carbohydrates, particularly glycogen. Observations on living sperm and spermatogenic cells from freshly prepared testis smears were made with Nomarski differential-interference optics.

Nuclear proteins were stained with alkaline (pH 8.3) fast green (HUMASON, 1967), alkaline (pH 8.3) eosin Y (BLOCH & HEW, 1960) or bromphenol blue adjusted to pH 2.3 with acetic acid (BLOCH & HEW, *op. cit.*). Prior to staining, nucleic acids were removed from tissue sections with trichloroacetic acid at 99°C for 30 minutes or with a saturated aqueous solution of picric acid at 60°C for 24 hours (BLOCH & HEW, *op. cit.*). These acid hydrolysis treatments usually resulted in the sections detaching from the slides. Consequently, slides were coated with a thin coat of celloidin following removal of wax from the sections. Protein end groups were blocked by deamination (after removal of DNA by acid hydrolysis) with Van Slyke's reagent (HUMASON, *op. cit.*; BLOCH & HEW, *op. cit.*) or by acetylation (HUMASON, *op. cit.*).

For electron microscopy, testes and segments of seminal vesicles were excised from freshly opened, unrelaxed snails and treated in accordance with the methods described in the first paper of this series (WEST, 1978).

OBSERVATIONS

The cellular elements and the organization of the male reproductive system were considered in detail in the first paper of this series (WEST, 1978), and only the salient features of the genital system will be considered here. The testis lies on the distal portion of the visceral mass and consists of numerous seminiferous tubules (100-800 μ m in diameter) which are separated from each other by a thin stroma. These tubules join to form the single vas deferens which passes along the columellar side of the body. The posterior portion of the vas deferens functions as the seminal vesicle and is filled with spermatozoa throughout the year.

Explanation of Figures 1 to 5

Figure 1: Spermatogonia (S) clustered near basal cell (B) $\times 5000$

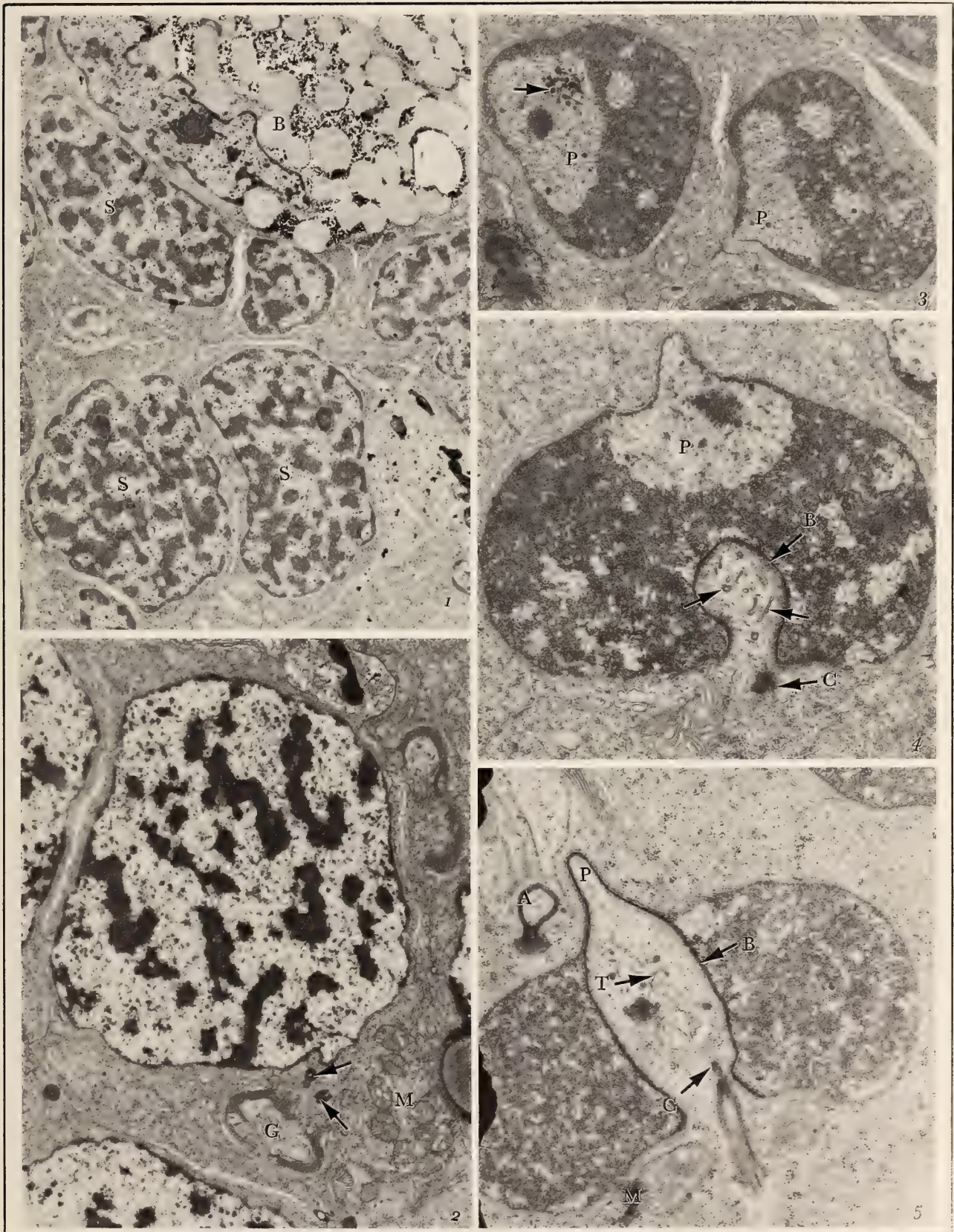
Figure 2: Primary spermatocyte. Arrows - centrioles; M - mitochondria; G - Golgi complex $\times 8500$

Figure 3: Early spermatid showing polar nucleoplasm (P) with small granules (arrows) and small patches of nucleoplasm $\times 11900$

Figure 4: Early spermatid at early flagellar tube formation. Arrows

- small tubules within flagellar tube; B - layer of condensed chromatin; C - centriole; P - polar nucleoplasmic cone $\times 18600$

Figure 5: Crescent-shaped spermatid. A - early acrosome with attached band of electron-dense material; B - layer of condensed chromatin; C - centriole; M - mitochondrion; P - flagellar tube projection; T - tubules within flagellar tube $\times 18600$



On the periphery of each seminiferous tubule, beneath the stroma, a layer of lipid-rich basal cells surrounds 2 types of accessory cells and the spermatogenic cells. Spermatogenic cells are generally clustered in small groups which are in the same maturation phase, and these groups of cells are irregularly distributed within the tubules. Spermatozoa generally fill the lumen of the tubule, but they also occur scattered between spermatogonia and spermatocytes.

Spermatogonia and Spermatocytes

Spermatogonia are difficult to distinguish from early spermatocytes. However, they stain intensely lavender with Lehman's polychrome stain and have irregularly shaped nuclei (Figure 1). Groups of spermatogonia (8 to 24 cells per group) generally occur near the periphery of seminiferous tubules, lying just beneath the layer of basal cells (Figure 1). Gonial cells measure 8 - 11 μm in diameter, and the nucleus (7 - 9 μm in diameter) occupies nearly the entire cell volume. The chromatin is unevenly distributed, giving the nucleus a patchy appearance, and the nuclear envelope is perforated by numerous, small pores. The single nucleolus is homogeneous and eccentrically located. Distributed within the moderately electron-dense nucleoplasm are numerous small granules. The scanty cytoplasm contains a few relatively long cisternae of rough endoplasmic reticulum and numerous, free ribosomes.

At the onset of spermatogenesis, spermatogonia increase in size to about 15 μm in diameter, giving rise to primary spermatocytes. Primary spermatocytes (Figure 2) have a small amount of cytoplasm surrounding the subspherical nucleus (11 - 13 μm in diameter) and, in addition to the elements found in spermatogonia, the cytoplasm contains several juxta-nuclear mitochondria. Situated near these mitochondria are 2 centrioles and a prominent Golgi complex (Figure 2). The chromatin is condensed and synaptonemal complexes which are concomitant with synapsed chromosomes (PARCHMAN & ROTH, 1971) are frequently observed. First and second meiotic divisions apparently occur in rapid succession, and secondary spermatocytes are rarely seen.

Spermiogenesis

Nucleus: Following the second meiotic division, the nuclear material of the early spermatid is coarsely granular and irregularly distributed throughout the nucleus, leaving small, irregular patches of granular nucleoplasm. Occasionally, cytokinesis is not complete and 2 or 4 early spermatids are joined by cytoplasmic bridges. However, later spermatids are not joined. As spermiogenesis pro-

ceeds, the nucleus increases in size, to about 7 μm in diameter, and is irregular in outline. The coarsely granular chromatin is irregularly distributed within the nucleus, leaving a large area of nucleoplasm (polar nucleoplasm) near the nuclear envelope and several, small patches irregularly distributed throughout the nucleus (Figure 3). The polar nucleoplasm (Figure 3) contains many small, electron-dense granules (0.1 - 0.2 μm in diameter) and a single, large granule (0.6 - 1.0 μm in diameter). The initial location of the polar nucleoplasm within the nucleus appears to be random (see Figures 3 and 12), but at the beginning of flagellar migration (see below), regardless of its initial position, the polar nucleoplasm moves to the anterior pole forming a cone-shaped projection (Figure 4). As nuclear maturation continues, the centriole and the elongating flagellum migrate through the nucleus, advancing within a cytoplasmic tube (flagellar tube) which is surrounded by the nucleus, and the polar nucleoplasm is lost, probably by extrusion of nucleoplasm (Figure 5). The remaining cone-shaped projection is somewhat smaller in size than the nucleoplasmic cone and composed of a thin layer of nuclear material enclosing the anterior end of the flagellar tube (Figure 5). Concurrent with the loss of the polar nucleoplasm, the posterior pole of the nucleus forms a shallow depression, and 2 mitochondria which form the middle piece (see below) move into this depression (Figure 5). In side view, at this phase of development, the nucleus is crescent-shaped with a small, anterior projection, and in side view it is doughnut-shaped.

As maturation continues, the nucleus assumes a spherical shape, about 7 μm in diameter, and is slightly flattened at the posterior pole (Figure 6). During this rounding phase, the coarsely granular chromatin of the crescent-shaped nucleus condenses into randomly oriented filaments which are about 50 \AA in diameter (Figure 7). Chromatin condensation occurs rapidly near the nuclear envelope and is initiated at the site of flagellar tube formation (see below). This condensation is concurrent with flagellar tube formation and, following flagellar tube formation, proceeds around around the periphery of the nucleus, resulting in a thin layer (170 - 180 \AA thick) of dense material appressed against the inner aspect of the nuclear envelope (see Figures 5 and 9). As maturation proceeds, the nucleus elongates to about 10 μm in length, and the filamentous chromatin forms dense aggregates through lateral association of the filaments. During further nuclear elongation (about 16 μm in length) the nuclear filaments fuse together, forming thick fibers (Figure 8). With further condensation, these thick fibers fuse, forming lamellae which are about 500 \AA thick (Figure 9). These lamellae are helically arranged in the long axis of

the nucleus and, at this stage of maturation, are loosely associated with each other. During further elongation, the lamellae become thicker and in closer association (Figure 10). Nuclear elongation and chromatin condensation continue until, in the mature sperm, the chromatin is homogeneous (Figure 11) and the nucleus is about $100\text{ }\mu\text{m}$ in length and $0.6\text{ }\mu\text{m}$ in diameter. Excess cytoplasm is eliminated and the nucleus surrounds the flagellum (Figure 11) with little space between the nuclear envelope and the axoneme. The plasmalemma is appressed to the nuclear membrane and is thrown into many small folds irregularly distributed around the nucleus (Figure 11).

Acrosome: In the early spermatid, a conspicuous Golgi complex is situated near the presumptive posterior pole of the nucleus (Figure 12) and consists of 12 - 15 gently curved saccules. Many small vesicles which are associated with the tips of the Golgi lamellae accumulate on the concave side of the complex and form a small, electron-dense proacrosomal granule (Figure 13). As nuclear condensation ensues, the Golgi complex, along with the proacrosomal granule, migrates to the anterior pole of the nucleus. During this migration the acrosome is elaborated by the Golgi complex and is essentially completed before nuclear elongation begins. During the migration phase, the Golgi lamellae become sharply curved and are shaped like an inverted V.

Golgi vesicles fuse with the proacrosomal granule which increases in size. Further addition of material to the proacrosomal granule occurs primarily at the presumptive anterior end of the acrosome (Figure 14), and the fusing Golgi vesicles form a membrane-limited, closed or somewhat open electron-dense ring (Figure 15, see also Figure 5). At the end of the migration phase (spherical nucleus stage) the early acrosome is situated near the nuclear envelope at the anterior pole, between the nucleus and Golgi complex. The early acrosome is shaped like a blunt cone with a small indentation at the base and has a small, electron-dense layer of material just beneath it. The blunt, anterior end of the acrosome is attached to the ring of

electron-dense material (Figure 15). During further maturation the acrosome elongates, and the indentation in its base becomes deeper, forming a cone-shaped space (subacrosomal space). The layer of electron-dense material just beneath the base widens and flattens, forming a plate (subacrosomal plate) between the acrosome and the nucleus (see Figure 8). During this stage of maturation, the acrosome ($0.025\text{ }\mu\text{m}$ wide and $0.3\text{ }\mu\text{m}$ long) becomes situated directly over the centriole at the anterior end of the nucleus. About the time the nucleus assumes a spherical shape, the band of electron-dense material associated with the acrosome separates from it and moves away, along with the Golgi complex (see Figure 8).

During the nuclear elongation phase, the acrosome elongates slightly and becomes more acute. The mature acrosome (Figure 16) sits over the subacrosomal plate, elevated by about $0.03\text{ }\mu\text{m}$. The subacrosomal plate abuts upon the nuclear envelope and is perforated by a single hole which is about $0.1\text{ }\mu\text{m}$ in diameter. The subacrosomal plate is situated over the centriole and a small anterior portion of the centriole, which is covered by a thin layer of nuclear material, penetrates this hole (Figure 17). The acrosome is about $0.8\text{ }\mu\text{m}$ in length and $0.3\text{ }\mu\text{m}$ in diameter at the caudal end, tapering anteriorly to about $0.04\text{ }\mu\text{m}$ in diameter. The subacrosomal space is approximately $0.35\text{ }\mu\text{m}$ long by $0.1\text{ }\mu\text{m}$ in diameter. Appressed to the outer acrosomal membrane are a layer of electron-dense material and the plasmalemma which together form a dense lamina over the acrosome (Figure 16). Near the anterior end of the acrosome (about $\frac{1}{4}$ of the distance from the apex) the dense lamina is separated from the acrosome, leaving a small space between it and the acrosome. This space is similar to the vesicle associated with the acrosome of *Thais lapillus* reported by WALKER (1970).

Flagellum: In the early spermatid, a single centriole is situated in the posterior pole cytoplasm near the Golgi complex (Figure 12). At the onset of tail formation, a thickening of nuclear material occurs on the inner aspect

Explanation of Figures 6 to 11

Figure 6: Round-stage spermatid. A - early acrosome; F - flagellar tube; G - Golgi complex $\times 10\,000$

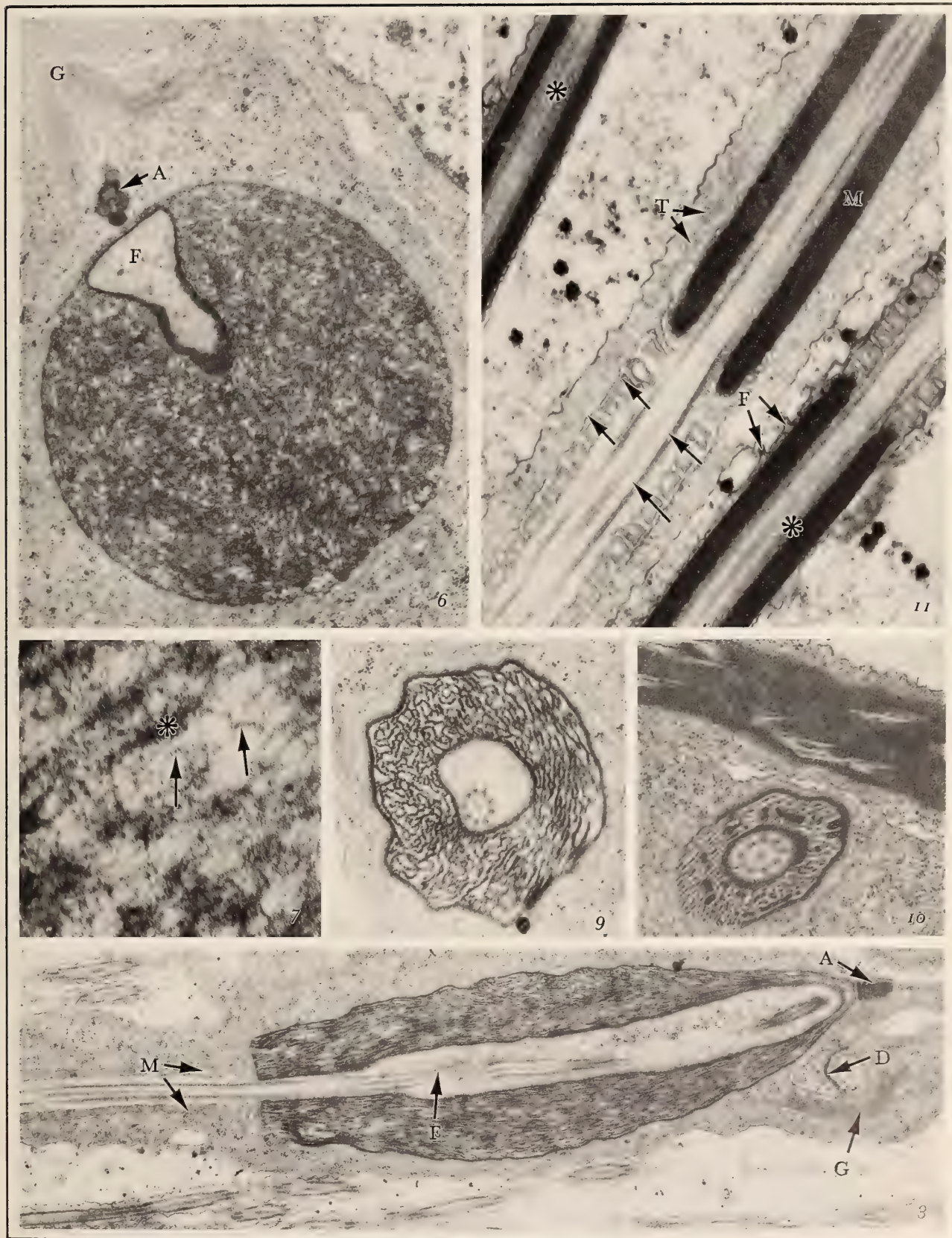
Figure 7: Filamentous chromatin (arrows) forming aggregates (*) $\times 112\,800$

Figure 8: Longitudinal section through elongating spermatid with thick fibrous chromatin. A - acrosome; D - dense material associated with early acrosome; F - flagellum; G - Golgi complex; M - middle piece $\times 10\,000$

Figure 9: Cross section of elongating spermatid with helically arranged nuclear lamellae $\times 16\,800$

Figure 10: Cross section and portion of longitudinal section through late-stage elongating nucleus with thickened nuclear lamellae $\times 15\,300$

Figure 11: Longitudinal section through portion of mature sperm (*) and sperm in final maturation stage (M). F - folds in plasmalemma; Arrows - indicate spiral arrangement of mitochondrion of mid-piece; T - microtubules comprising manchette $\times 12\,400$



of the nuclear membrane (Figure 12) opposite the centriole. This condensation is initiated at the site of the ultimate attachment point of the flagellum. During maturation, nuclear material is further condensed on the inner aspect of the nuclear membrane, lining the flagellar tube, and proceeds around the periphery of the nucleus. At the site of the initial condensation the nucleus invaginates and the polar nucleoplasmic cone is formed (Figure 4). The nuclear envelope follows the contour of the nucleus and also lines the invaginated area. This process continues, forming a tube (flagellar tube) through the center of the nucleus. The invagination process terminates when the posterior pole nuclear membrane is juxtaposed to the anterior pole membrane. These membranes are separated from each other by the layer of homogeneous, condensed chromatin (170 - 180 Å thick) and a thin layer (about 250 Å thick) of granular chromatin (Figure 5). During the final phase of flagellar tube formation, the polar nucleoplasmic cone is lost and the resulting projection covers the anterior end of the flagellar tube (Figure 5). About the time the flagellar tube is completed, the centriole with the elongating flagellar axoneme moves into the flagellar tube, preceded by several small tubules (Figures 4 and 5). The centriole migrates within the cytoplasm of the flagellar tube and moves to the anterior end of this tube, abutting upon the outer aspect of the nuclear membrane which lines the flagellar tube (Figure 18). The small tubules preceding the centriole are lost by the end of centriolar migration, which is about the time the nucleus assumes a spherical shape. The centriole serves as the basal body of the flagellum and is composed of a circle of 9 triplet tubules. Connecting the centriole to the nucleus is an electron-dense connecting piece which is about 0.12 μm wide and 0.12 μm long (Figure 18). Together, the connecting piece and centriole are similar in appearance to basal bodies of cilia and flagella.

The flagellum is surrounded by the nucleus in the head region and by the mitochondrion in the middle piece. The principal piece, beginning just below the middle piece, is packed with glycogen particles which surround the axoneme (Figure 19). The axoneme has the typical 9 + 2 configuration of tubules. The end piece (1 - 2 μm in length) is tubular and devoid of axonemal elements and glycogen.

Middle Piece: Four to 6 mitochondria are present in the cytoplasm of the early spermatid, near the Golgi complex and centriole. As nuclear condensation begins and the flagellar tube is formed, these mitochondria fuse and form 2 large mitochondrial derivatives. These 2 derivatives move into a depression in the posterior pole of the nucleus which is at about the stage of the crescent-shaped

nucleus (Figure 5). These 2 mitochondria wrap around the flagellar axoneme and elongate posteriorly. During the initial elongation phase, the mitochondrial cristae are randomly oriented. The mitochondria form a loose spiral around the flagellar axoneme and are separated from it by a thin layer of cytoplasm. The mitochondria elongate to about 10 μm in length and their outer membranes fuse forming a common outer membrane. The cristae are reorganized and become stacked in a periodic array, and the inner membranes retain their individuality. In the mature middle piece (Figure 19) the mitochondrial elements appear tightly spiraled around the axoneme (Figures 11 and 19) and the inner mitochondrial membranes are closely apposed to the outer circle of flagellar fibers.

Manchette: The manchette is formed during the final elongation and nuclear condensation phases and is composed of 3 - 5 concentric rows of microtubules which are oriented in the long axis of the spermatozoa (Figure 11). The rows of microtubules do not completely surround the spermatozoon and are biradially arranged (Figure 20), generally lying perpendicular to the 2 central fibers of the axoneme. The inner-most row contains the largest number of tubules (15 - 20), and proceeding outward, the number of tubules per row decreases to 3 - 5.

Mature Spermatozoon: The mature spermatozoa of *Colus stimpsoni* are morphologically identical. They are filiform and measure 137 - 140 μm in length. The head is about 100 μm long, and the middle piece is between 7 and 10 μm in length. The remaining portion, 25 - 30 μm long, constitutes the principal and end pieces. The head tapers from about 0.3 μm in diameter at the anterior end to about 0.7 μm at its caudal end. The middle piece is uniform in diameter, about 0.7 μm , throughout its length. The principal piece tapers from 0.7 μm in diameter to about 0.4 μm at the end piece. The short end piece is about 0.03 μm in diameter. The anterior $\frac{5}{8}$ of the principal piece contains glycogen particles which surround the axoneme. The axoneme extends from the anterior end of the head, attaching just beneath the acrosome, to within 2 μm of the posterior-most end of the spermatozoon and is surrounded by the nucleus, middle piece and glycogen particles along its length.

Cytochemistry

Results from cytochemical techniques employed to categorize nuclear proteins indicate that a transition in these components occurs during spermiogenesis. Following removal of DNA with hot trichloroacetic acid (TCA), the nuclei of mature spermatozoa and late spermatids stain with bromphenol blue, alkaline fast green and alkaline

eosin Y, but early and middle stages do not. After TCA treatment and deamination with Van Slyke reagent which affects the epsilon amino groups of lysine, the various stages of spermiogenesis stain the same as when treated with TCA alone. The dye-binding ability of histones which have a high arginine-to-lysine ratio is relatively unaffected by deamination, and the above results suggest the presence of an arginine-rich histone(s) in the late spermatids and spermatozoa.

Following extraction of DNA from tissue sections with mild acid hydrolysis (aqueous picric acid), all stages of spermiogenesis retain the dyes employed. These results

suggest the presence of a protamine(s) which is extracted with the TCA method. After mild hydrolysis and deamination, only the late spermatids and mature spermatozoa retain the dyes. These results suggest the presence of a lysine-rich protamine(s) in the early and middle stages of spermiogenesis. Table 1 gives the results of the nuclear protein staining procedures.

The combined results of all cytochemical procedures suggest that a transition from a lysine-rich protamine(s) to an arginine-rich histone(s) occurs during spermiogenesis. This transition occurs at about the time of nuclear elongation in which the thick chromatin fibers fuse and form

Table 1

Results of Nuclear Protein Cytochemistry

Technique	Spermatids			Spermatozoa	
	Early	Middle	Late	Testicular	Seminal Vesicle
<i>TCA Hydrolysis</i>					
Bromphenol Blue	—	—	+	+	+
Eosin Y	—	—	+	+	+
Fast Green	—	—	+	+	+
<i>Deamination</i>					
Bromphenol Blue	—	—	+	+	+
Eosin Y	—	—	+	+	+
Fast Green	—	—	+	+	+
<i>Picric Acid Hydrolysis</i>					
Bromphenol Blue	+	+	+	+	+
Eosin Y	+	+	+	+	+
Fast Green	+	+	+	+	+
<i>Deamination</i>					
Bromphenol Blue	—	—	+	+	+
Eosin Y	—	—	+	+	+
Fast Green	—	—	+	+	+

+, positive reaction; —, negative reaction

Explanation of Figures 12 to 20

Figure 12: Early spermatid at beginning of flagellar tube formation. B — thickening of nuclear material in inner aspect of nuclear envelope; C — centriole; G — Golgi complex; P — polar nucleoplasm $\times 9600$

Figure 13: Proacrosomal granule (arrow) within early spermatid $\times 19000$

Figure 14: Proacrosomal granule (arrow) during migration phase $\times 19000$

Figure 15: Early acrosome (*) with attached band of electron-dense material (D); P — early subacrosomal plate $\times 20500$

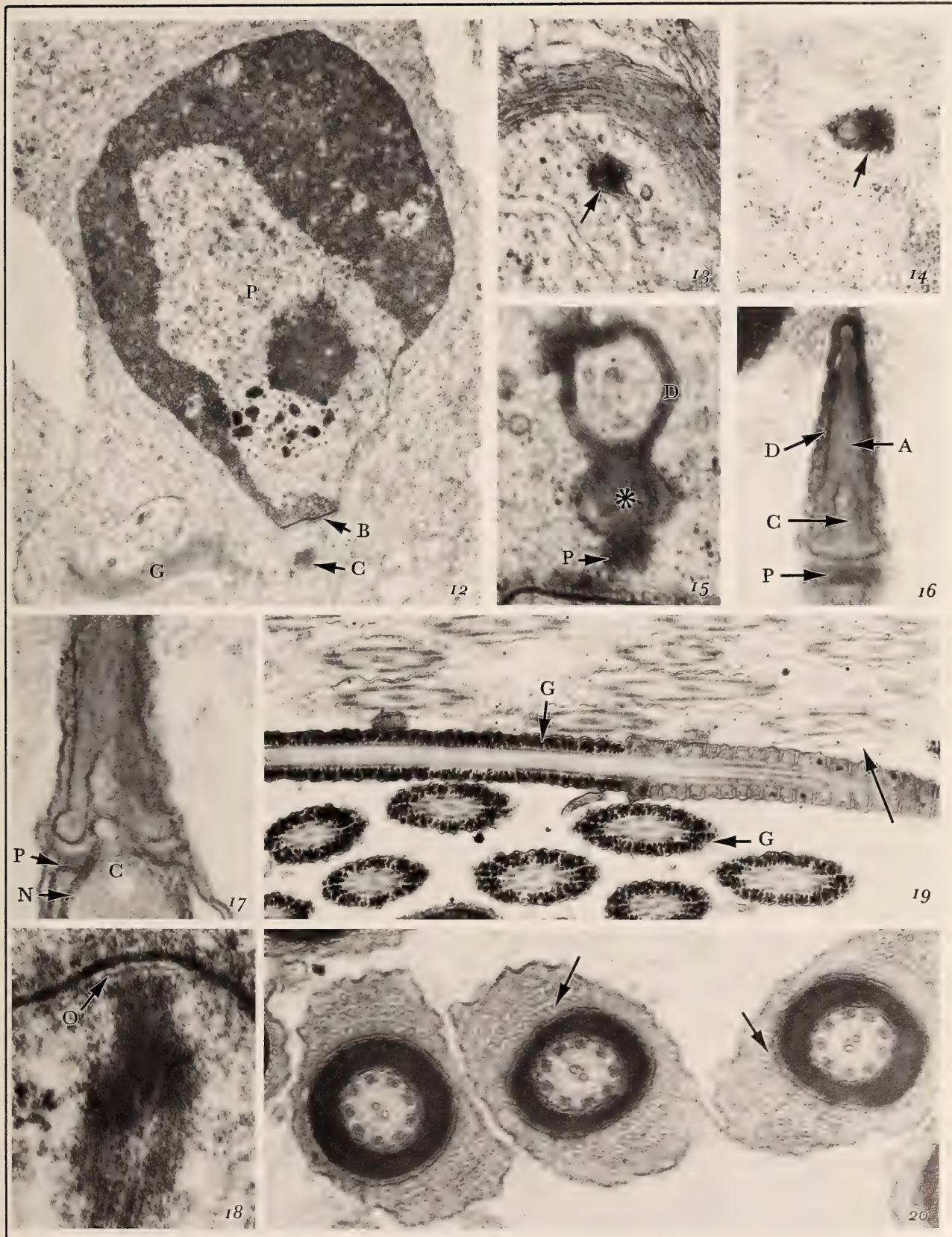
Figure 16: Longitudinal section through mature acrosome (A). C — subacrosomal space; D — dense lamina covering acrosome; P — subacrosomal plate $\times 47000$

Figure 17: Oblique longitudinal section through posterior portion of acrosome. C — flagellar connecting piece; N — nuclear material; P — subacrosomal plate $\times 73000$

Figure 18: Longitudinal section through flagellar connecting piece. O — outer aspect of nuclear membrane $\times 73000$

Figure 19: Portions of middle piece and principal piece. Arrows show spiral arrangement of mitochondrion. G — glycogen within principal piece $\times 19200$

Figure 20: Cross section through nucleus showing disposition of microtubules (arrows) comprising the manchette $\times 48000$



lamellae. However, this time course is estimated from length measurements related to the nuclear events observed by electron microscopy and is only an approximation.

DISCUSSION

In *Colus stimpsoni*, as in other animals, the spermatogenic cells are confined in compartments (seminiferous tubules) which isolate them from somatic tissue. Spermatogenic cells occur in clusters which are in the same maturation stage. Prior to giving rise to primary spermatocytes, spermatogonia presumably undergo a few mitotic divisions, since almost all metazoa exhibit premeiotic spermatogonial divisions (ROOSEN-RUNGE, 1969). However, the number of spermatogonial divisions in *C. stimpsoni* is unknown. The low number of secondary spermatocytes observed suggests that the 2 meiotic divisions occur in rapid succession.

The meiotic divisions result in spermatids which contain the haploid number of chromosomes, and separation of these chromosomes divides them equally among daughter cells. No evidence of chromosome elimination or diminution was observed. PORTMANN (1931) reported that a pair of chromosomes are somewhat isolated from the remaining chromosomes at the equatorial plate during meiosis I in the eupyrene sperm line in *Buccinum undatum* Linnaeus and *Thais lapillus* (Linnaeus), but he did not follow the behavior of this pair of chromosomes. KUSCHAKIEWITSCH (1924) suggested that this chromosomal arrangement is widespread among prosobranchs, but WALKER & MACGREGOR (1968) and WALKER (1970) made no mention of this chromosomal condition in their studies of spermatogenesis in *Thais lapillus*. This chromosomal arrangement was not observed in either of the meiotic divisions of *Colus stimpsoni*, nor was any variant of this condition found.

Spermiogenesis in *Colus stimpsoni* is essentially similar to that described in other mollusks and in some insects (TUZET, 1930; FRANZEN, 1955; KAYE, 1958; DUPOUY, 1964; WALKER & MACGREGOR, 1968; CHEVAILLIER, 1970). Following the second meiotic division, nuclear condensation ensues and the spermatids undergo morphogenetic changes which result in the final mature sperm. Various factors have been implicated in the shaping of the sperm head. Aggregation of the filamentous nuclear material in early spermatids leads to the nuclear lamellae observed in late spermatids. It has been suggested, since these nuclear threads are similar in size in many animals, that they may be the ultimate nucleo-protein units in the chromosomal structure (GALL & BJORK, 1958). GALL & BJORK (*op. cit.*)

suggested that lamellar formation is through the lateral association of these fine filaments and that the centriole may act as a center for the organization of the nuclear material in the long axis of the sperm head. In *C. stimpsoni* the unusual condition of the flagellum completely penetrating the long axis of the sperm head, resulting in the sperm nucleus forming a cylinder, may impose certain restrictions upon the distribution of the nuclear material. However, the role of the centriole and its relation to the pattern of nuclear condensation is unclear. Other workers (KESSEL, 1970; CLARK, 1967; MCINTOSH & PORTER, 1967) have suggested that the microtubules of the manchette may be involved in shaping the sperm head. In *C. stimpsoni* the arrangement of the manchette superficially suggests a structural function for the manchette. However, the manchette does not appear until the nuclear material is almost condensed into its final shape.

During spermiogenesis in most animals, there is a change in the nuclear proteins (BLOCH & HEW, 1960; HNILICA *et al.*, 1971). BLOCH & HEW (*op. cit.*) have shown that there is a transition from a lysine-rich histone to an arginine-rich protamine during spermiogenesis in the pulmonate *Helix aspersa* Müller, 1776. WALKER & MACGREGOR (1968) reported a transition from a lysine-rich histone to an arginine-rich histone during sperm maturation in *Thais lapillus* and indicated that the change in histone composition coincided with the formation of the nuclear lamellae. In *Colus stimpsoni* a transition of nuclear proteins occurs during spermiogenesis which is similar to that of *Thais lapillus*. However, in *C. stimpsoni* the transition is from a lysine-rich protamine(s) in the early spermatid to an arginine-rich histone(s) in the late spermatid and mature sperm. This transition appears to coincide with the formation of the nuclear lamellae. The results of this study support the supposition that microtubules are not directly involved in shaping the sperm head and that the shape may be determined by a genetically controlled pattern of aggregation of DNA and nuclear proteins. The involvement of the histone component in the aggregation of DNA and the final shaping of the sperm head has been proposed (ZIRKIN, 1971; FAWCETT *et al.*, 1971). However, the extent to which nuclear proteins are involved remains unknown.

The mature sperm of *Colus stimpsoni* is filiform in shape and is classified as "modified" type for internal fertilization according to FRANZEN's (1955, 1970) scheme. The condition of the flagellum extending through the sperm head has been reported for other closely related species of neogastropods (RETZIUS, 1906; PORTMANN, 1931; FRANZEN, 1955). The sperm head in *C. stimpsoni* is rather long, comprising about 70% of the total sperm length. The acrosome is insignificant in size in relation to the sperm

head and is similar to the acrosome of *Thais lapillus* described by WALKER & MACGREGOR (1968). The mitochondrion of the mid-piece is modified from the "primitive" type (FRANZEN, 1955; FAVARD & ANDRÉ, 1970) and lacks glycogen granules. However, the principal piece is packed with glycogen granules. The presence of glycogen granules in sperm tails seems to be widespread in animals (ANDERSON & PERSONNE, 1970).

Spermiogenesis in *Colus stimpsoni* follows the typical pattern found in many animals. In many prosobranch species, more than one morphological type of sperm has been reported (TUZET, 1930; PORTMANN, 1931; BULNHEIM, 1962; TOCHIMOTO, 1967; RETZIUS, 1906; DUPOUY, 1964). *Thais lapillus* does not exhibit sperm dimorphism (WALKER & MACGREGOR, 1968; RETZIUS, 1906). However, PORTMANN (1931) reported differences in nuclear condensation during spermatogenesis in *T. lapillus* and suggested that sperm dimorphism in this species is of a physiological nature. These differences were not mentioned by WALKER & MACGREGOR (*op. cit.*) in their ultrastructural studies in spermatogenesis in *T. lapillus*. The occurrence of a physiological dimorphism in *C. stimpsoni* is possible. However, the present evidence does not suggest this, and it is proposed that the sperm in *C. stimpsoni* are all of the eupyrene type.

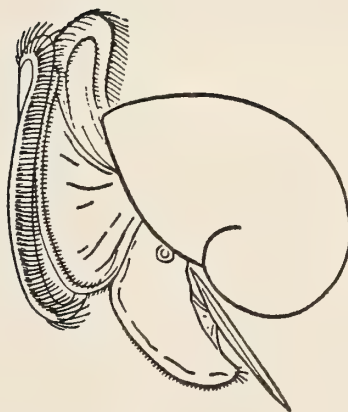
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The Ultrastructure and Evolutionary Significance of the Cerebral Ocelli of *Mytilus edulis*, the Bay Mussel

BY

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(4 Plates; 3 Text figures)

INTRODUCTION

Mytilus edulis Linnaeus, 1758, the bay mussel, has circum-boreal distribution and is usually found in protected coastal waters. The life history includes planktonic trochophore, veliger, and pediveliger stages (FIELD, 1922). At a length of 240 - 245 μ m, the veliger larvae develop a pair of eyes immediately posterior to the prototroch and innervated by the cerebral ganglia (BAYNE, 1964). Veligers with eyes display positive phototaxis until they approach metamorphosis, at which time they become negatively phototactic (BAYNE, *op. cit.*). The paired cerebral eyes do not atrophy during metamorphosis, as originally reported by Lovén but persist throughout life (PELSENEER, 1899, 1908).

Among bivalves, cerebral eyes are distributed throughout several superfamilies including the Mytilacea, Pterinea, Arcacea, Anomiaea, and Ostreaea (PELSENEER, 1908). According to a phylogenetic scheme presented by STASEK (1963), all of these superfamilies represent an evolutionary offshoot that diverged early from the main line of bivalvian evolution.

Pallial eyes, located on the exposed mantle edges, are more conspicuous than cerebral eyes and have been described at an ultrastructural level in the following groups: Pectinacea (BARBER *et al.*, 1967), Cardiacea (BARBER & WRIGHT, 1969a), Tridacnacea (KAWAGUTI & MABUCHI, 1969), Arcacea (LEVI & LEVI, 1971), Pandoridae (ADAL & MORTON, 1973). Except for the Arcacea and Pectinacea, bivalves with pallial eyes represent more recently evolved groups than do bivalves with cerebral eyes (STASEK, 1963). Although the presence and position of eyes were not taken into account in the construction of Stasek's phylogenetic scheme, his analysis reflects the probability that cerebral eyes existed in bivalves prior to pallial ones.

Accordingly, the cerebral eyes of bivalves may be homologous to those of the other molluscan classes, as well as to those of the other major invertebrate groups. Thus, one would expect greater similarity among the cerebral eyes of various mollusks than between cerebral and pallial eyes of bivalves.

The evolutionary significance of the fine structure of invertebrate eyes and photoreceptors has been discussed by EAKIN (1963, 1965, 1968), LAND (1968), HERMANS (1969), HERMANS & EAKIN (1974), WOLKEN (1974), ERMAK & EAKIN (1975), VANFLETEREN & COOMANS (1976), and others. Although all organelles thought to be photoreceptive are composed of membranous systems providing relatively large surface areas, EAKIN (1963, 1972) postulated that there are 2 distinctive types of photoreceptors: ciliary and rhabdomeric.

In ciliary photoreceptors, the membranous systems are formed from sensory cilia that typically lack a central pair of microtubules in the axonemes, and are referred to as 9+0. The outer membranes of these cilia give rise to the tubules, lamellae, sacs, discs, and other structures that form the photoreceptor organelles (EAKIN, 1972). In rhabdomeric photoreceptors the organelles consist of microvilli that develop from membranous projections and invaginations of the plasmalemmas of the photoreceptor cells, not of the plasmalemmas of cilia.

EAKIN (1968) further postulated that ciliary photoreceptors are predominantly characteristic of the deuterostomous line of evolution, whereas the protostomous phyla are largely characterized by rhabdomeric photoreceptors. However, a number of inconsistencies have been demonstrated in that not all photoreceptors in protostomes are rhabdomeric and not all photoreceptors in deuterostomes are ciliary.

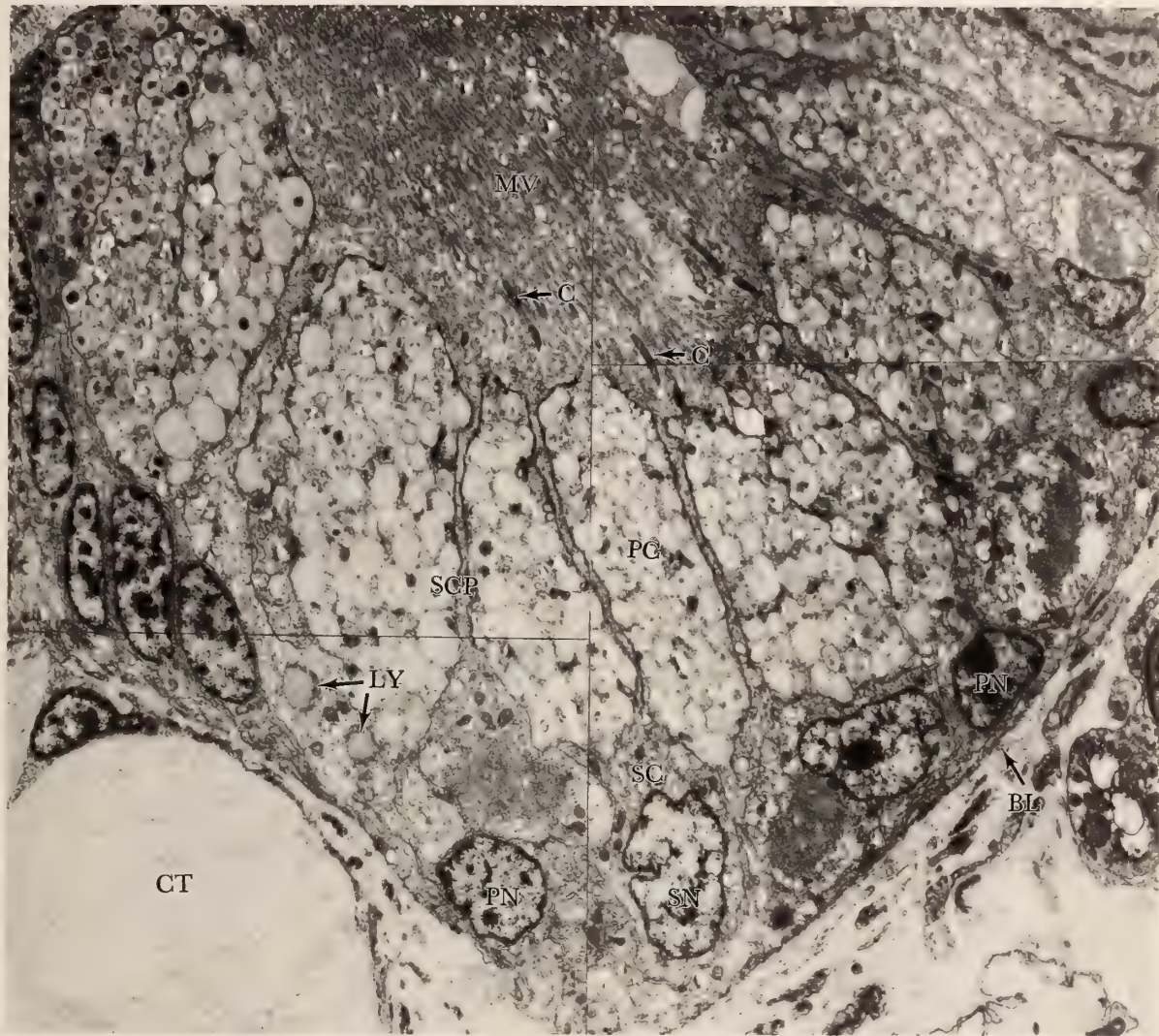


Figure 3

Low magnification electron micrograph of a transverse section through an ocellus showing the shape and arrangement of the sensory cells (SC), pigment cells (PC), and the rhabdomeric microvilli (MV). BL - basal lamina; CT - connective tissue; SCP - sensory cell process; LY - lysosomes; PN - pigment cell nucleus; SN - sensory cell nucleus; C - cilia

×4500

In contrast to Eakin, VANFLETEREN & COOMANS (1976) believed the differences between ciliary and rhabdomeric photoreceptors to be more of quantitative than of qualitative order. Those authors suggested on the basis of diverse evidence that the formation of both types of photoreceptors is initially induced by cilia, with the cilia being partially to completely aborted in rhabdomeric types. Thus, Vanfleteren & Coomans concluded that the type of photoreceptor is not conservative or distinctive enough for evaluating evolutionary relationships between phyla.

The presence of the same type of photoreceptor in ocelli that would not otherwise be considered homologous suggests that photoreceptor type is a trait that could have been convergently evolved. This means that homology must first be determined at an ocellar, or organ level rather than at a photoreceptor, or organelle level. Some authors have noted that the ultrastructural similarities among the cerebral ocelli of various sipunculans, mollusks, annelids, and onychophorans extend beyond the resemblance of their rhabdomeric photoreceptors (HERMANS, 1969; HERMANS & EAKIN, 1974; ERMAK & EAKIN, 1975). These cerebral ocelli are regarded by those workers as likely to be homologous. Thus, cerebral eyes may provide a coherent line of evidence with which to evaluate interphyletic relationships.

The purpose of this study is to offer the first ultrastructural description of the cerebral ocellus of a bivalve mollusk, to appraise its evolutionary significance, and to reassess the value of photoreceptors in the study of evolution.

We wish to express our appreciation to Dr. Richard M. Eakin for his counsel during the course of this investigation.

MATERIALS AND METHODS

Specimens of *Mytilus edulis* ranging in length from 3 mm to 3 cm were collected at Mason's Marina, Bodega Bay, Sonoma County, California. The mussels were either fixed immediately or maintained at 12°C in aquaria of unfiltered seawater.

Living mussels were bisected along the sagittal plane and placed in a fixative solution of 4% glutaraldehyde, 0.15M sodium cacodylate and 0.15M sodium chloride at room temperature and pH 7.3. After 30 minutes in this solution, the eyes were excised and transferred to a fresh solution of the same fixative for 1 hour; washed for 30 minutes in a solution of 0.15M sodium cacodylate and 0.15M sodium chloride at room temperature and pH 7.3; and post-fixed for 1 hour in ice cold 2% OsO₄, 0.15M sodium cacodylate and 0.15M sodium chloride at pH 7.3.

Dehydration in ethanol and propylene oxide was followed by embedding and sectioning in Epon.

For light microscopy, sections 1 μ m thick were mounted on glass slides and stained with 1% toluidine blue in 1% borax.

For electron microscopy, gold and silver ultrathin sections were collected on uncoated grids and stained in uranyl acetate and lead citrate. The sections were examined with a Zeiss EM 9A having an accelerating voltage of 60 kv.

RESULTS

General Anatomy

The paired cerebral eyes of *Mytilus edulis* are located at the bases of the first ctenidial filaments of left and right inner demibranchs (Figures 1 and 2, O). The eyes in living specimens are covered with mucus from the ctenidia, and each appears as a dark reddish-brown spot when viewed with a hand lens. The diameter of the eye is 40 - 50 μ m throughout the life of the mussel, with the result that the eyes of small specimens are more conspicuous than those of large ones.

Lateral to each eye is a triangular translucent zone in the anterior region of each valve (Figure 2, SW). These "shell windows" permit diffuse light to reach the eyes. In mussels less than 5 mm long, the entire shell is thin and translucent. In larger mussels, with thicker shells, only the shell windows remain translucent.

Microscopic Anatomy

Each ocellus is an "open cup" with no cornea or lens (Figure 6). The opening of the cup faces laterally into the space between the inner demibranch and outer palp (Figure 6, ID, OP). Cilia from adjacent feeding organs project into this space (Figure 6, C). A layer of fibrous connective tissue lies below the eye (Figure 6, CT). The retina, composed of sensory and pigment cells, has 3 distinct regions or layers: nuclear, pigmented, and photoreceptor (Figure 6, a, b, c). In the nuclear region, 8 μ m thick, both sensory and pigment cell nuclei are visible. The former are larger and stain lighter than the latter. In the pigmented region, 20 μ m thick, the pigment cells (Figure 6, PC) are broad and lightly stained, whereas the sensory cells (Figure 6, SC) are narrow and stain more darkly. The photoreceptor region is 15 μ m thick and consists of photoreceptor organelles that are directed toward incoming light rather than away from it. Thus, the ocellus is converse rather than inverse.

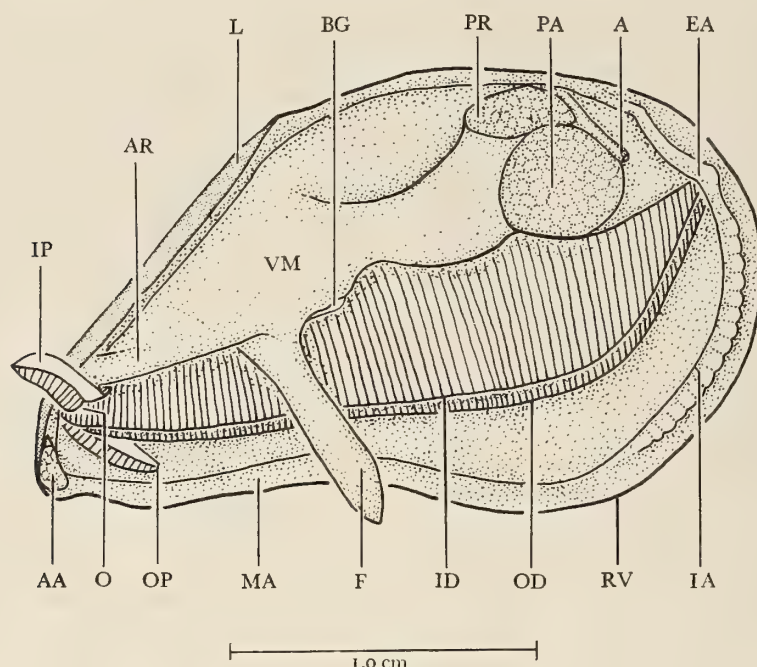


Figure 1

Side view of *Mytilus edulis* with left valve and pallial organs removed. The cerebral ocellus (O) (not visible) is located behind the inner palp (IP) at the base of the first filament of the inner demibranch (ID). AR - anterior retractor muscle; L - hinge

ligament; BG - byssus gland; VM - visceral mass; PR - posterior retractor muscle; PA - posterior adductor muscle; A - anus; EA - exhalant aperture; IA - inhalant aperture; RV - right valve; OD - outer demibranch; F - foot; MA - mantle; OP - outer palp; AA - anterior adductor muscle

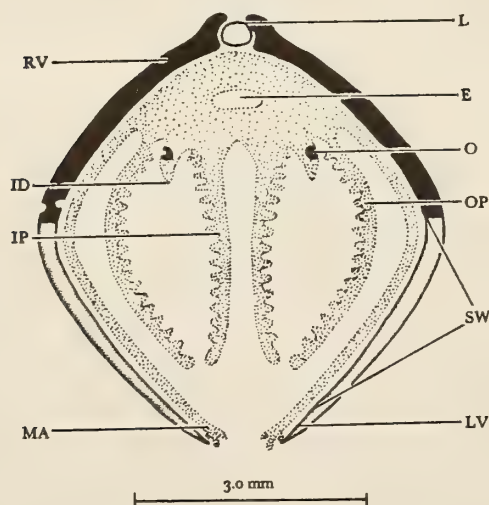


Figure 2

Transverse section through the first anterior filaments of left and right inner demibranchs (ID), showing the location of the ocelli (O) and shell windows (SW). E - esophagus; LV - left valve. See Figure 1 for additional symbols

Ultrastructure

The pigment and sensory cells interdigitate in an irregular manner (Figures 3 and 4). A basal lamina separates the retina and adjacent ciliated epithelium from the underlying connective tissue (Figure 3, BL, CT). The nuclear regions of the pigment cells average $3.0\mu\text{m}$ in width. Distal to the nuclear regions these cells are heavily pigmented and collectively form the pigment cup. Here, each cell is about $4.0\mu\text{m}$ wide. Pigment cell apices narrow to approximately $1.0\mu\text{m}$ and give rise to stubby microvilli that average $0.6\mu\text{m}$ in length and $0.13\mu\text{m}$ in diameter. The pigment cells are all close to $23\mu\text{m}$ long, including microvilli.

The sensory cells have bulbous nuclear regions that average $4.0\mu\text{m}$ in width. Distal to the nuclear region, slender sensory cell processes, approximately $0.3\mu\text{m}$ wide, occupy the spaces between the heavily pigmented areas of the pigment cells (Figure 3, SCP). Apically, sensory cells each expand to a width of about $3.0\mu\text{m}$ and give rise to the rhabdomeres, which consist of parallel arrays of undulating microvilli. Each microvillus is about $12\mu\text{m}$

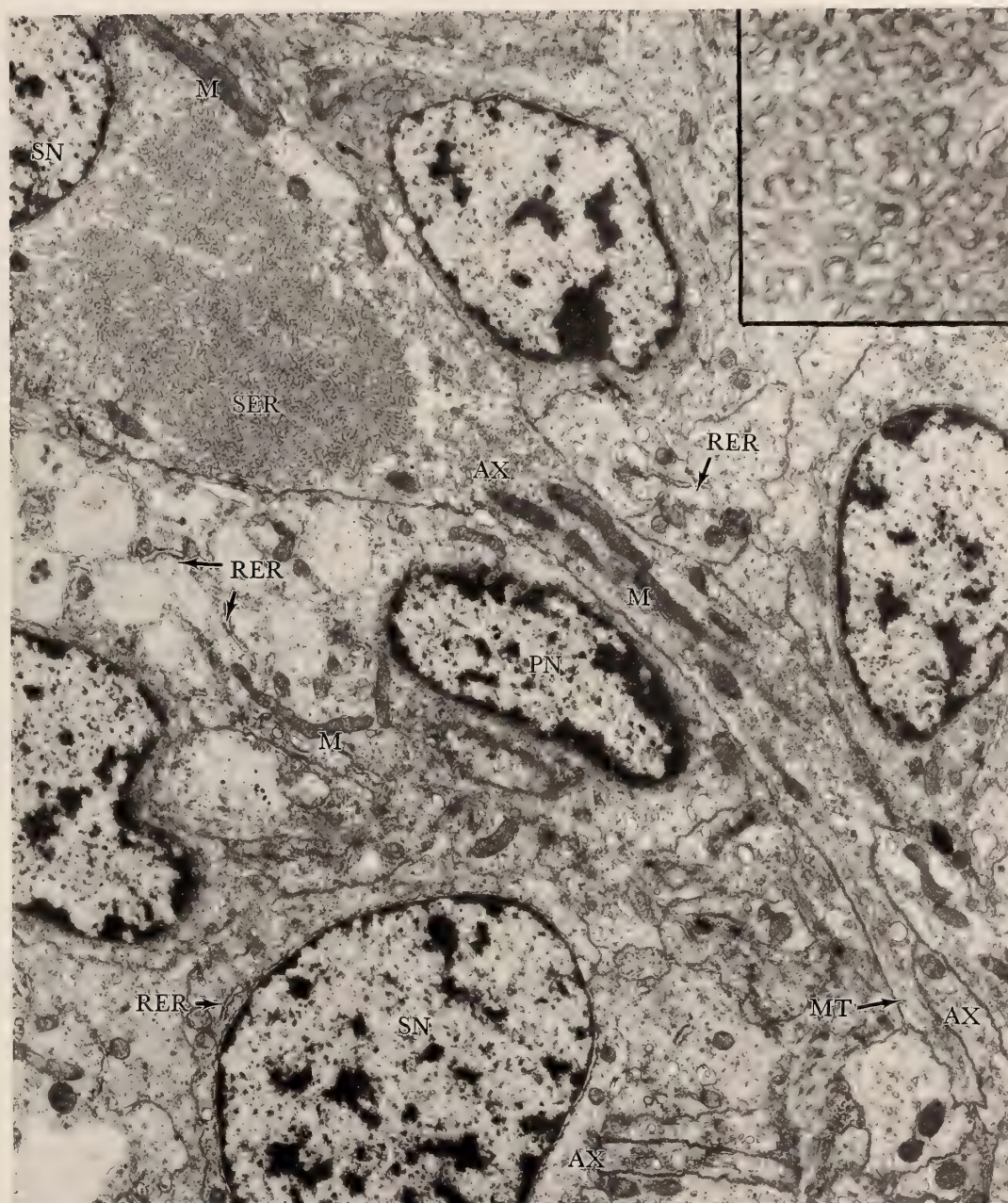


Figure 5

Nuclear region of the ocellus showing an axon (AX) in continuity with the proximal part of a sensory cell, and two other axons converging at lower right. M - mitochondria; RER - rough endoplasmic reticulum; SER - smooth endoplasmic reticulum; MT - microtubules; SN - sensory cell nucleus; PN - pigment cell nucleus.

× 10 000

Inset: Enlargement of unusual smooth endoplasmic reticulum (SER) × 38 000

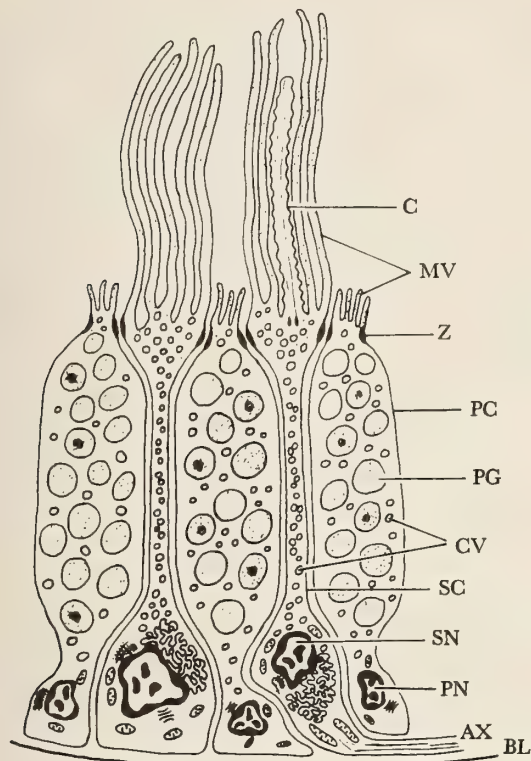


Figure 4

Part of retina illustrating the shape and arrangement of sensory cells (SC) and pigment cells (PC). C - cilium; MV - microvilli; Z - adhering zonule; PG - pigment granule; CV - cytoplasmic vesicles; SN - sensory cell nucleus; PN - pigment cell nucleus; AX - axon; BL - basal lamina

long and $0.16\mu\text{m}$ in diameter (Figures 3 and 12, MV). The overall length of these cells, including the rhabdomeres, averages $35\mu\text{m}$.

In sensory cells mitochondria are numerous only in the nuclear region (Figures 5 and 7, M). Membrane-bounded cytoplasmic vesicles are abundant distal to the nuclei (Figure 7, CV). Lysosome-like organelles have been occasionally observed (Figure 3, LY). Rough endoplasmic reticulum and an unusual type of smooth endoplasmic reticulum are frequently seen (Figure 5, RER, SER). The unusual smooth endoplasmic reticulum consists of irregular crenulations of 2 undulating membranes separated by a uniform space of 175\AA (Figure 5, inset). This organelle has only been observed close to the sensory cell nucleus. Axons originate from the proximal ends of the

sensory cells (Figure 5, AX). The axons contain numerous mitochondria, longitudinally oriented microtubules, and finely granular cytoplasm (Figure 5, M, MT).

Sensory cell processes contain numerous membrane-bounded cytoplasmic vesicles from 0.1 to $0.3\mu\text{m}$ in diameter, which have heterogeneously dense centers (Figure 8, CV). Longitudinally oriented microtubules and dense granules, averaging 400\AA in diameter, which are presumed to be beta particles of glycogen, were also observed (Figure 8, MT, GG).

Pigment cells contain fewer organelles than do sensory cells, with mitochondria and rough endoplasmic reticula occupying the nuclear regions (Figure 5). Distal to the nuclear region, pale membrane-bounded granules of shading pigment are the main constituents of these cells (Figures 7 and 8, PG). The pigment granules range from 0.7 to $2.0\mu\text{m}$ in diameter and their densities vary. Such granules are absent from the sensory cells. Dispersed throughout the pigment cells are membrane-bounded cytoplasmic vesicles similar to, but fewer in number than, those observed in sensory cells (Figure 8, CV).

Sensory and pigment cell apices are characterized by prominent adhering zonules and septate junctions (Figures 9, 10, and 11, Z, SJ). The septate junctions form borders between sensory cell processes and pigment cells that extend from the apices well into the pigmented region of the retina (Figures 9 and 10, SJ). Cytoplasmic vesicles are located at the apices of both cell types (Figures 10 and 11, CV). Some pigment cell apices contain unusually dense cytoplasm (Figure 10, DC). A single cilium, oriented parallel to the microvilli, is frequently observed originating from a sensory cell (Figure 11, C). Observed in cross section, such cilia clearly show the typical $9+2$ arrangement of microtubules in their axonemes (Figure 13, C). Cilia have not been observed to originate from pigment cells.

DISCUSSION

Structure

Cerebral ocelli of bivalve mollusks have been described at a light microscopical level by PELSENEER (1899, 1908), FIELD (1922), and others, as cited by BAYNE *et al.* (1976). PELSENEER (1908) compared the cerebral eyes of 30 closely related bivalves and found their structure to be similar and their location uniform. Both Pelseener and Field concluded that the ocelli of mussels are well developed and capable of directional sensitivity to light. Both of these authors, however, described a cuticular lens which the present electron micro-

scopical investigation demonstrates to be the array of photoreceptor microvilli. The ocellar cavity has no cuticular covering. The ocelli of *Mytilus* are "open cups" similar to those of *Haliotis* (TONOSAKI, 1967) and *Nautilus* (BARBER & WRIGHT, 1969b) in which the ocellar cavities are exposed directly to seawater.

In the absence of a lens, the ocellus of *Mytilus* is not so well-developed as Pelseneer and Field concluded. Well-developed invertebrate eyes, presumed to be capable of forming images, typically possess a lens such as that found in the pelagic polychaete *Vanadis tagensis* Dales, 1955 (HERMANS & EAKIN, 1974). In contrast to this, the eye of *Nautilus*, a primitive cephalopod, lacks a lens but is able to cast inverted images onto the retina by means of a pinhole aperture (BARBER & WRIGHT, 1969b; WOLKEN, 1971). Lacking a lens or pinhole aperture, the ocellus of *Mytilus* is not capable of forming images. Nevertheless, it is possible that the ocelli give *Mytilus* limited sensitivity to the direction of illumination, as interpreted from the regular organization of the microvillous rhabdomeres and the concavity of the retinas.

Functions of the sensory and pigment cells are directly related to their differing forms (Figures 3 and 4). The broad apices of the sensory cells give rise to the microvilli, which are presumed to be photoreceptor organelles (EAKIN, 1972). Slender sensory cell processes, passing through the pigmented region, contain microtubules and numerous cytoplasmic vesicles as supportive or transportive elements (EAKIN, 1972). These processes are without pigment granules and therefore do not function as shading elements. The relatively wide nuclear regions of the sensory cells house rich accumulations of mitochondria and both smooth and rough endoplasmic reticula. The presence of these organelles indicates the high level of synthetic activity common to visual cells (EAKIN, *op. cit.*). Pigment cells are narrow apically and bear microvilli that

are and presumed to be of a supportive function. These cells are maximally broad in the pigmented region, forming the pigment cup whose presumed function is that of shading the rhabdomeres from light in all but one direction. It is unlikely that the pigment cup also serves as a reflecting layer, for it lacks the characteristics of a tapetum (EAKIN, *op. cit.*). The reduced number of organelles in the pigment cells indicates a level of synthetic activity lower than that in sensory cells.

The interdigitation of sensory and pigment cells is not entirely regular. Two or more cells of the same type are occasionally observed together. This irregularity is also found in some gastropods: *Littorina scutulata* Gould, 1848 (MAYES & HERMANS, 1973); *Haliotis discus* Reeve, 1846 (TONOSAKI, 1967); *Littorina littorea* Linnaeus, 1758; *Nucella emarginata* Lamarck, 1819; *Lacuna* sp.; *Tegula funebris* Adams, 1854 (all in BAKER, 1975); *Helix aspersa* Müller, 1774 (EAKIN & BRANDENBURGER, 1967a). In the retinas of squids and octopuses, however, the interdigitation is regular; there is a single pigmented-supportive cell for every tetrameric rhabdome (ZONANA, 1961; TONOSAKI, 1965). A relatively uncommon feature of retinas composed of interdigitating sensory and pigment cells is the total lack of pigment granules in the sensory cells. The ocelli of certain gastropods (EAKIN, 1968) and of the sea star *Asterias rubens* Linnaeus, 1758 (VAUPEL-VON HARNACK, 1963) share this feature with *Mytilus*, as well as a marked similarity in the arrangement and relative form of the retinal cells.

Red pigment granules are common to the ocelli of *Mytilus*, of the protist *Euglena* (WOLKEN, 1967), and of the sea stars *Henricia leviuscula* Stimpson, 1857 (EAKIN, 1968) and *Asterias rubens* Linnaeus, 1758 (VAUPEL-VON HARNACK, 1963). When fixed in glutaraldehyde, red pigment granules tend to appear very pale (EAKIN, 1972). A red, water-soluble substance, taken from the ocelli of

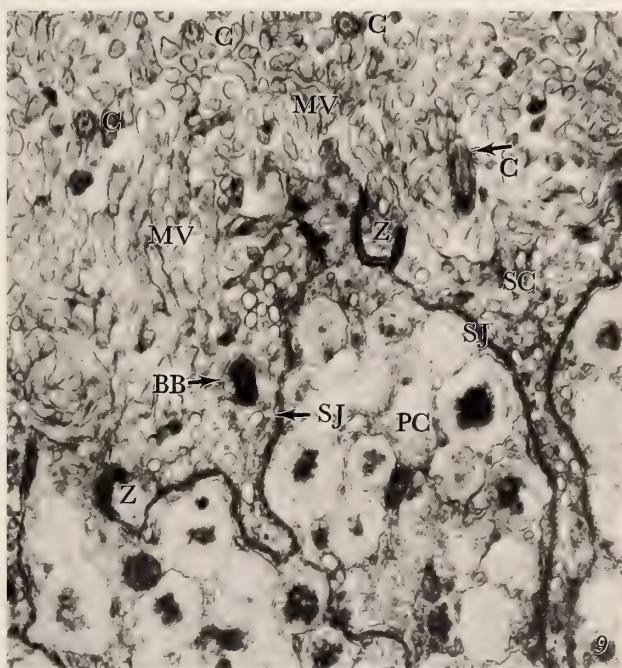
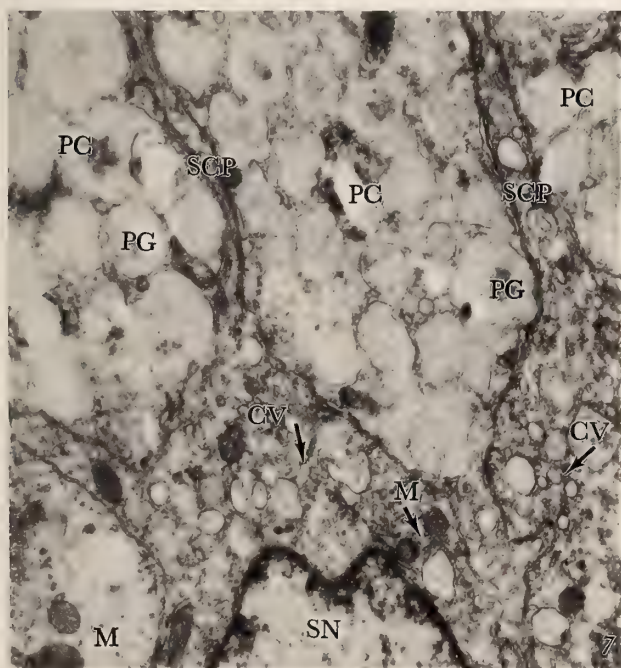
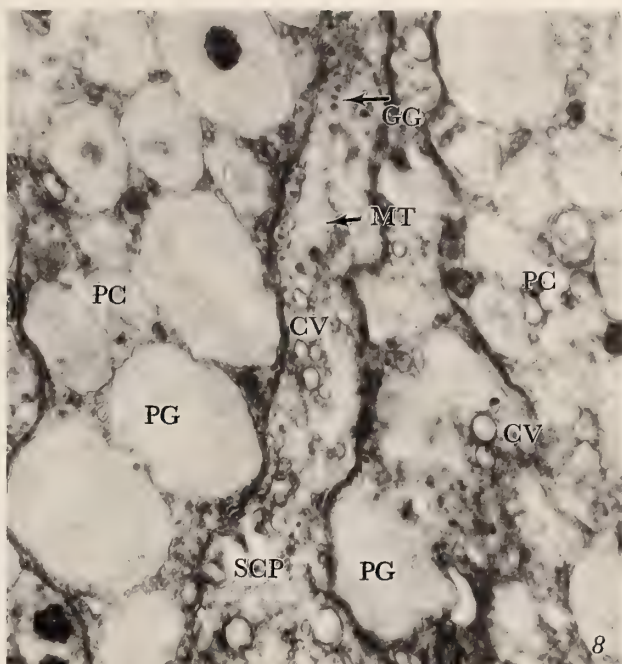
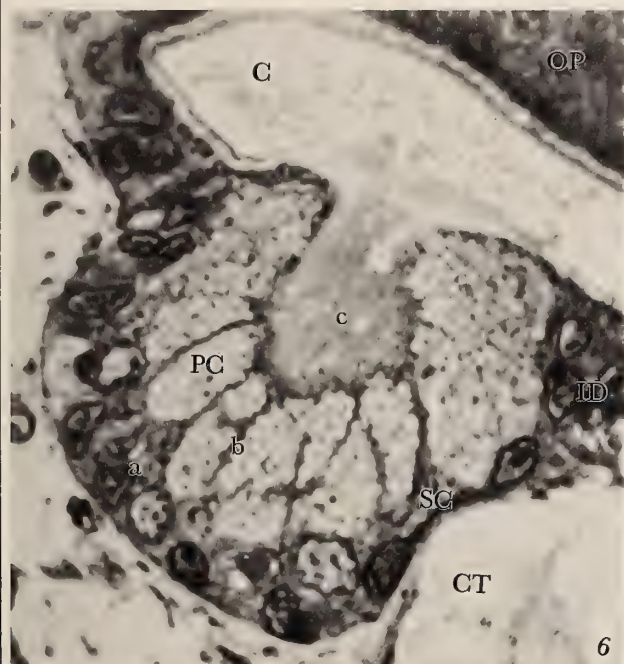
Explanation of Figures 6 to 9

Figure 6: Light micrograph of a transverse section through an ocellus and adjacent structures: outer palp (OP); inner demi-branch (ID); and connective tissue (CT). Three distinct layers are visible within the ocellus: nuclear (a); pigmented (b); and photoreceptor (c). C - cilia; PC - pigment cell; SC - sensory cell
× 1 400

Figure 7: Nuclear region of ocellus showing a portion of a sensory cell nucleus (SN) and 2 sensory cell processes (SCP). M - mitochondria; CV - cytoplasmic vesicles; PG - pigment granule; PC - pigment cell
× 11 000

Figure 8: Pigmented region of the ocellus showing a sensory cell process (SCP) between 2 pigment cells (PC). CV - cytoplasmic vesicles; MT - microtubules; GG - glycogen granules; PG - pigment granule
× 14 000

Figure 9: Apices of pigment and sensory cells (PC, SC). A presumptive ciliary basal body (BB) can be seen at the apex of one sensory cell. Adhering zonules (Z) and septate junctions (SJ) are prominent in this region. MV - microvilli; C - cilia
× 14 000



the sea star *Asterias amurensis* Ives, 1891, was found to yield carotenoids upon denaturation (YOSHIDA & OHTSUKI, 1966) which suggests that carotenoids may be the shading pigments of red ocelli. Electron dense granules of shading pigment, thought to be melanin (EAKIN, 1972), are more common among invertebrates than are these red granules.

The cilia found in the mussel retina have the form of 9+2 kinocilia with arms rather than of 9+0 sensory cilia. Numerous other ocelli with rhabdomeric photoreceptors also possess 9+2 cilia that may originate from sensory cells, pigment cells, or both (EAKIN *et al.*, 1967; TONOSAKI, 1967; HUGHES, 1970; JACKLET *et al.*, 1972; MAYES & HERMANS, 1973; BOYLE, 1969; BAKER, 1975). Cilia in the retina of *Mytilus* possibly serve a cleansing function, such as preventing mucus laden with debris from fouling the rhabdomeres. These cilia are not regarded as photosensitive structures, and further research is needed before these cilia can be considered as the inducers of photoreceptor formation (VANFLETEREN & COOMANS, 1976).

Unusual accumulations of smooth endoplasmic reticulum found in the nuclear regions of the sensory cells (Figure 5) are similar in form to the smooth endoplasmic reticulum found in the eye of the garden slug *Limax maximus* Linnaeus, 1758 (EAKIN & BRANDENBURGER, 1975). In *Limax*, however, this membranous organelle has always been observed in the distal ends of sensory cells in several separate formations rather than in one large accumulation as in *Mytilus*. EAKIN & BRANDENBURGER (*op. cit.*) cited several other instances in which this special endoplasmic reticulum has been described. Its occurrence is not restricted to eyes. At the time of their publication, EAKIN & BRANDENBURGER (*op. cit.*) were attempting to link this special endoplasmic reticulum to calcium transport, but conclusive evidence was not obtained. In *Mytilus*, it is likely that this special endoplasmic reticulum serves as a synthesizing organelle; however, further research is needed to determine its function.

The membrane-bounded cytoplasmic vesicles observed in the sensory cells are similar to the spherical vesicles in other molluscan photosensory cells described by EAKIN *et al.* (1967), TONOSAKI (1967), HUGHES (1970), MAYES & HERMANS (1973), and BAKER (1975). The eyes of the pulmonates described by EAKIN & BRANDENBURGER (1967a, 1975) contain sensory cell vesicles that are organized into paracrystalline arrays and have been termed photic vesicles by those authors. Photic vesicles carry photopigment, or precursors thereof, from Golgi bodies, from which they originate, to the bases of the microvilli (EAKIN & BRANDENBURGER, 1967b, 1974). The presence and arrangement of cytoplasmic vesicles in *Mytilus* and other molluscan eyes suggest similar functions.

Behavioral Role

Young, eyed, veliger larvae of *Mytilus* display positive phototaxis. Older, pediveliger larvae are negatively phototactic and settle with the anterior end oriented away from light (BAYNE, 1964). In larval mussels, it is possible that the cerebral eyes provide the directional sensitivity to light.

In an attempt to relate the presence of eyes to the biology of *Mytilus*, simple field and laboratory observations of post-larval mussels have revealed no behavioral responses indicative of light sensitivity. In the field, the direction of illumination, or the absence of direct illumination does not obviously affect the orientation of individuals, pattern of clumping, distribution of clumps, or filter-feeding activities. Simulated predation by shadow-casting, or sudden intense illumination directed upon the shell windows did not stop the pumping activity of gaping mussels, whereas even slight tactile stimulation applied with the blunt end of an applicator stick to the exposed mantle tissues or shell, resulted in the closure of gaping mussels.

HARGER (1968) reported another instance in which other senses predominate over that of light sensitivity in mussels. That author described a "crawling out" behavior in *Mytilus edulis* but not in *M. californianus* Conrad, 1837, the sea mussel. Where both species occurred together on pier piles, *M. edulis* was more prominent on the outside of clumps. Under laboratory conditions, *M. edulis* consistently "crawled out" from under 5 cm of pea-sized gravel whereas *M. californianus* did not. Neither the direction of illumination, nor the absence of it, affected this response. HARGER (*op. cit.*) considered "crawling out" behavior an adaptation that prevents bay mussels from becoming smothered by silt, which is not a problem for sea mussels exposed to wave action.

Although no correlation between the presence of the ocelli and photic response could be made, 3 anatomical features suggest that the eyes remain functional in post-larval mussels. First, the overall structure of the ocellus is that of a photosensitive organ. Next, the presence of axons and synthesizing organelles indicates that the ocellus is engaged in sensory activity. Finally, the "shell window" allows the eye to receive illumination. PELSENEER (1908) stated that several of the 30 species he studied possess a triangular translucent zone in the anterior region of each valve and suggested that this allows the eyes to remain functional. An example of functional light transmission through a molluscan shell has been described recently. LINDBERG *et al.* (1975) demonstrated that the nocturnal limpet *Notoacmea persona* (Rathke, 1833) is negatively phototactic, a behavior mediated by light strik-

ing the eyes through translucent zones in the anterior region of the shell.

In addition to the "shell windows," PELSENEER (1908) observed conditions among the cerebral eyes of bivalves that indicate that these eyes are only present when they can be functional, that is, in the presence of light. *Pinctada* and *Anomia* bear larvae with paired cerebral eyes. As these bivalves mature, they become fixed to the bottom with the right side adjacent to the substratum, and the eye on that unilluminated side subsequently atrophies whereas the eye on the illuminated side persists. Species of *Dacrydium*, of the family Mytilidae, live in the aphotic zone and are without eyes. *Modiolaria trapezina* Lamarck, 1819, also a mytilid, has larvae that are incubated within the mantle cavities of the adults, and this species lacks eyes throughout its life history. Apparently, natural selection conserves cerebral eyes only when they are of some functional value.

What, then, is the function of these ocelli? The lack of immediate behavioral responses to light suggests that the eyes in post-larval mussels may function in some long term response, such as mediating photoperiod in the reproductive cycle. This hypothesis may find support in the work by ELVIN (1976), who demonstrated that neurosecretory release by the cerebral ganglia in sexually mature specimens of *Mytilus edulis* is enhanced by the presence of light.

Evolutionary Significance

A. Homology of Molluscan Cerebral Eyes

The cerebral eyes of bivalves and the larval eyes of chitons develop in the region immediately posterior to the prototroch (PELSENEER, 1908; HEATH, 1904). Because of their location, these eyes have not been considered homologous to the pre-trochal cerebral eyes of the Gastropoda, or to the cephalic eyes of the Cephalopoda, which are without a larval stage (PELSENEER, 1908; RAVEN, 1966). There are, however, structural similarities among the

ocelli of bivalves, gastropods, and cephalopods that indicate that the prototroch may be of secondary importance with respect to ocellar homologies. Ultrastructural investigations to date have demonstrated that molluscan cerebral eyes have similar retinas composed of interdigitating pigment and sensory cells with microvillous rhabdomeres borne at the distal ends of sensory cells. Additionally, the cerebral ganglia of these classes develop from similar cephalic plates (RAVEN, 1966), and innervation of the cerebral eyes is directly from the cerebral ganglia whether the eyes develop in the pre- or post-trochal region (FIELD, 1922; RAVEN, *op. cit.*). These characteristics indicate that the cerebral eyes of the bivalves are homologous to those of the gastropods and cephalopods.

The larval eyes in chitons have been considered by PELSENEER (1899) as likely to be homologous to the cerebral eyes of bivalves, on the basis of their similar, post-trochal locations. HEATH (1904), however, stated that these two groups of ocelli are fundamentally different in structure and noted that the innervation of the chiton ocellus is from the pallial nerves. Thus, an ultrastructural description of the larval eyes in chitons would be useful in determining whether these eyes are similar to the cerebral eyes of the other molluscan classes, and is now in progress¹.

PELSENEER (1908) stated that he labeled cerebral eyes as "cephalic eyes" in 1899 to distinguish them from pallial eyes, even though he did not consider the former to be homologous with the eyes of cephalopods and gastropods. Also in 1908, Pelseeneer changed his term for these eyes from "yeux cephaliques" to "yeux branchiaux." Apparently, Pelseeneer made this change in terminology to main-

¹ Note added in proof: One of us (M. D. R.) has begun preliminary observations on the ultrastructure of ocelli in the larvae of *Katharina tunicata*, obtained through the courtesy of Dr. Dale B. Bonar at Friday Harbor Laboratories, Summer of 1977. The ocellus consists of several pigment cells and at least one sensory cell. The presumptive photoreceptors are rhabdomeric microvilli that originate at the distal end of the sensory cell.

Explanation of Figures 10 to 13

Figure 10: Three adjacent pigment cell apices. Arrows indicate origins of microvilli (MV). Dense cytoplasm (DC) is occasionally observed at pigment cell apices. Z - adhering zonule; SJ - septate junction; CV - cytoplasmic vesicles

× 29 000

Figure 12: Photoreceptor microvilli (MV) and cilia (C) in the ocellar cavity

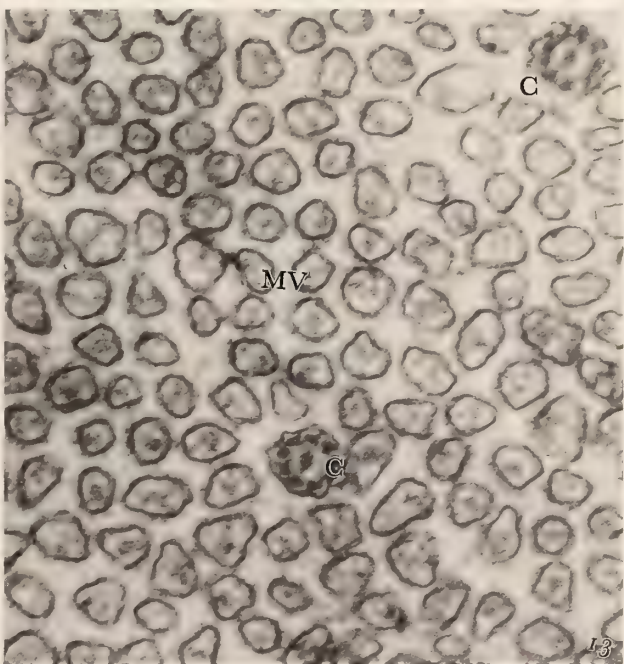
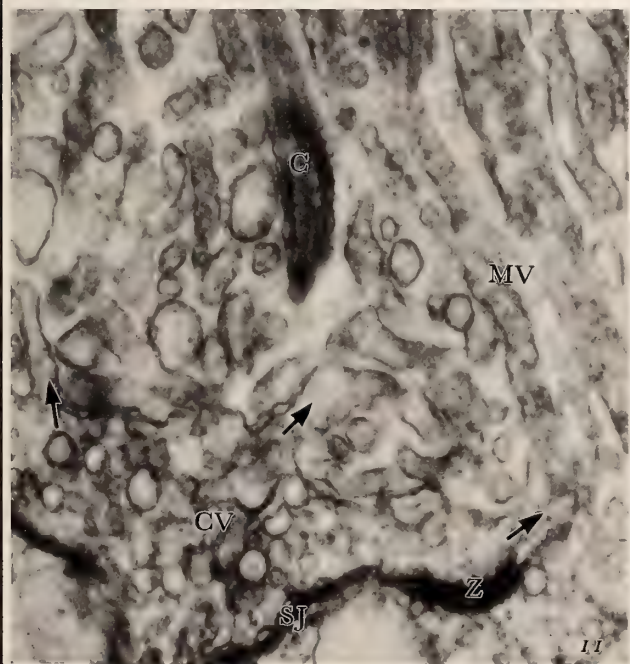
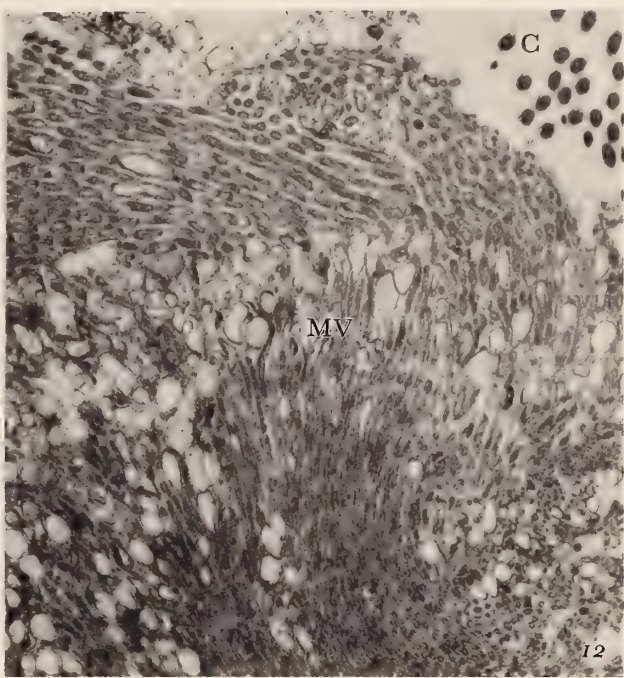
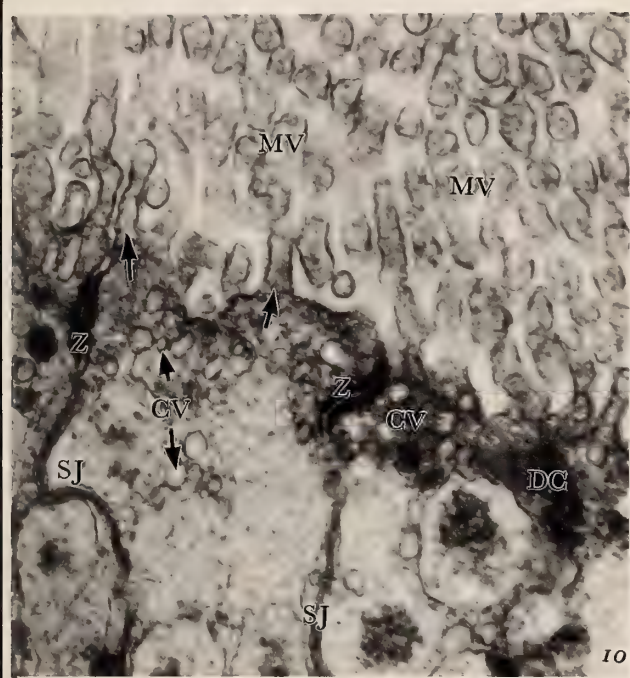
× 10 000

Figure 13: Microvilli (MV) and sensory cell cilia (C) in cross section

× 38 000

Figure 11: Sensory cell apex. Arrows indicate origins of microvilli (MV). A cilium (C) may be originating from this cell. Z - adhering zonule; SJ - septate junction; CV - cytoplasmic vesicles

× 29 000



tain the continuity of his phylogenetic scheme in which modern families of bivalves were conceived to have evolved from one another on the basis of increasing complexity of their gills (see family tree in PELSENEER, 1911: 123). His stated reasons for this revision were 1) the eyes are situated on the branchial filaments, and 2) the Recent nuculid protobranchs, considered by Pelseeneer to be the ancestral bivalves, lack these eyes in all stages of development. Hence, he concluded that the cerebral eyes in mytilids could not have been inherited from these protobranchs and must therefore be recently evolved specializations. Our re-interpretation is as follows: 1) The eyes are found on the first branchial filaments of post-larval mussels (Figure 6) but originate in the larvae prior to the formation of these filaments; 2) the gills are innervated by the visceral ganglia (FIELD, 1922), indicating that the eyes, which have cerebral innervation, are not fundamentally branchial; 3) although the protobranchs are considered primitive on the basis of gill type by PELSENEER (1911) and gill to palp association by STASEK (1963), their lack of eyes does not necessarily reflect a primitive condition, but rather a secondary loss since all modern species occupy deep-water or infaunal habitats where cerebral ocelli would have no functional role.

B. Ciliary Photoreceptors

versus Rhabdomic Photoreceptors

All the eyes of bivalves previously studied by electron microscopy have contained photoreceptor organelles that are derived from modified cilia (BARBER *et al.*, 1967; BARBER & LAND, 1967; BARBER & WRIGHT, 1969a; KAWAGUTI & MABUCHI, 1969; LEVI & LEVI, 1971; ADAL & MORTON, 1973). The photoreceptors of these eyes have therefore presented exceptions to Eakin's postulation that rhabdomic photoreceptors are typical of the protostomous phyla (EAKIN, 1968). However, there is no evidence that pallial eyes are homologous with cerebral eyes. Therefore, the occurrence of ciliary photoreceptors within pallial ocelli is here regarded as immaterial to the present evolutionary hypotheses concerning cerebral ocelli.

Rather, the cerebral ocelli of *Mytilus* contain rhabdomic photoreceptors, as well as other ultrastructural features that conform to the structural patterns found in the cerebral ocelli of hitherto studied species of mollusks, sipunculans, annelids, and onychophorans, as noted by HERMANS (1969), HERMANS & EAKIN (1974), and ERMAK & EAKIN (1975). Thus, judged from the groups examined to date, photoreceptor type is conserved in cerebral ocelli and does aid in establishing the broad evolutionary affinities among the protostomous phyla.

The cerebral eye of the heteropod *Pterotrachea mutica*, as described by DILLY (1969), may represent an exception to the apparent conservatism in the structure of photoreceptors in the cerebral ocelli of the protostomes. Dilly considered the photoreceptors of this eye to be of the ciliary type, but his evidence is not convincing (see EAKIN, 1972: 629-630).

C. Evolution and Function

LAND (1968) concluded from behavioral and electrophysiological data that eyes with ciliary photoreceptors typically respond to cessation of illumination or to shadows and usually function in protection from predatory attack. In contrast, eyes with rhabdomic photoreceptors typically respond to the onset of illumination and function by monitoring light intensity. VANFLETEREN & COOMANS (1976) considered this correlation between photoreceptor type and ocular function as a generalization with a few known exceptions. Moreover, we regard this pattern as a potential explanation for the selective pressures that may have led to the presence of either ciliary or rhabdomic photoreceptors in non-cerebral ocelli.

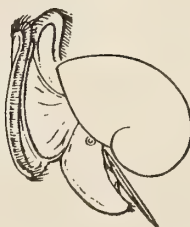
CONCLUSION

The cerebral ocelli of *Mytilus edulis* bear rhabdomic photoreceptors and conform in this way to the cerebral ocelli of all other protostomous classes hitherto described. The diversity in structure and location of non-cerebral ocelli indicates that as a group they are not homologous sense organs. Yet, the similarities among certain groups of ocelli, such as the branchial eyes of sabellid polychaetes, may be useful in studying relationships at low taxonomic levels, as suggested by VANFLETEREN & COOMANS (1976). On the other hand, we are suggesting that the cerebral ocelli of the protostomes are all homologous and are useful for studying relationships at high taxonomic levels.

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The Genus *Lepidozona*

(Mollusca : Polyplacophora)

in the Temperate Eastern Pacific, Baja California to Alaska, with the Description of a New Species

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(5 Plates; 3 Text figures)

THE GENUS *Lepidozona* Pilsbry, 1892, is remarkably well represented in the eastern Pacific. In addition to the 6 species recognized in the Panamic province (FERREIRA, 1974), some twenty other nominal species of chitons in the northeastern Pacific have been assigned to the genus.

This study continues previous work on the tropical eastern Pacific *Lepidozona* (FERREIRA, *l.c.*), and extends the review of the genus to the temperate waters of the Californian, Oregonian, and Aleutian provinces which, covering some 6000 km of coast from Baja California to Alaska, lie between the parallels 23°N and 60°N approximately. The investigation is based upon the examination of material in the collections of the California Academy of Sciences (CAS), Los Angeles County Museum of Natural History (LACM), Allan Hancock Foundation (AHF), University of Southern California (UCLA), San Diego Museum of Natural History (SDNH), United States National Museum of Natural History (USNM), Academy of Natural Sciences of Philadelphia (ANSP), and in the private collections of Allyn G. Smith (AGS), John H. Himmelman, S. Stillman Berry (SSB), Salle Crittenden, George A. Hanselman, Glenn & Laura Burghardt, and myself (AJF).

From the data, 8 species of *Lepidozona* are recognized in the temperate northeastern Pacific, one new to science:

Lepidozona cooperi (Dall, 1879)

Lepidozona guadalupensis Ferreira, spec. nov.

Lepidozona mertensii (Middendorff, 1847)

Lepidozona pectinulata (Carpenter in Pilsbry, 1893)

Lepidozona retiporosa (Carpenter, 1864)

Lepidozona scabricostata (Carpenter, 1864)

Lepidozona sinudentata (Carpenter in Pilsbry, 1892)

Lepidozona willetti (Berry, 1917)

POLYPLACOPHORA de Blainville, 1816

Neoloricata Bergenhayn, 1955

ISCHNOCHITONINA Bergenhayn, 1930

ISCHNOCHITONIDAE Dall, 1889

Lepidozona Pilsbry, 1892

As redescribed (FERREIRA, 1974: 163): Small to medium size chitons. End valves and lateral areas with radial ribs, usually pustulose or graniferous; central areas with longitudinal riblets, often cross-ribbed (latticed), the jugal tract usually diverging forwardly to form a wedge-like feature on the second valve. Articulation usually white; end valves with around 10 slits; intermediate valves uni-slitted; sutural laminae sharp; eaves not spongy; sinus well defined. Girdle of imbricated, medium size scales, usually strongly convex, striated, and mammillated.

Type species: *Chiton mertensii* Middendorff, 1847, by OD, PILSBRY, 1892: 125.

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Lepidozона mertensii (Middendorff, 1847)

(Figures 1, 2, 20, 21, 34)

Chiton Mertensii MIDDENDORFF, 1847a: 118*Chiton (Stenosemus) Mertensii*, MIDDENDORFF, 1847b: 125 - 127, tbl. 14, figs. 1 - 3*Lepidopleurus mertensii*, COOPER, 1867: 22 - DALL, 1879: 332*Ischnochiton mertensii*, PILSBRY, 1892: 125 - 126, plt. 26, figs. 20 - 26, (in section *Lepidozона*); 1898, 50: 288 - HEATH, 1904, 56: 257 - 259, textfig. B; 1905, 29: 391 - NIERSTRASZ, 1905, 48: 82 - BERRY, 1907, 21 (5): 51 - DALL, 1921, 112: 192 (in section *Lepidozона*) - OLDROYD, 1924: 191 - 192; 1927: 280 - 281 - JOHNSON & SNOOK, 1927: 564 - SIMROTH & HOFFMAN, 1929: 314 - CHACE & CHACE, 1930, 44 (1): 8; 1933, 46 (4): 124 - FRASER, 1932, 3rd ser., 26 (5): 65 - LELOUP, 1940: 10 - 12, figs. 25 - 33 - WILLETT, 1941: 185 - 186, fig. 1 - ANDREWS, 1945, 26: 24 - 37 - LA ROCQUE, 1953: 12 (in section *Lepidozона*) - LIGHT, et al., 2nd ed., 1954: 217 - 218 - THOMPSON & CHOW, 1955, 3 (suppl.): 20 - 39 - THORPE, 1962, 4 (4): 205, 207 - HELFMAN, 1968, 10 (3): 290 - 291*Ischnochiton (Lepidozона) mertensii*, BERRY, 1917, 7 (10): 26; 1922, 11 (18): 475 - 476, plt. 10, figs. 7 - 12 (fossil); 1927, 17: 164 - A. G. SMITH, 1947: 18 - A. G. SMITH & GORDON, 1948, 26 (8): 208 - ABBOTT, 1954: 322 - 323*Lepidozона mertensii*, IS. TAKI, 1938: 390 - 392, plt. 14, fig. 6; plt. 29, figs. 1 - 6; plt. 30, figs. 6 - 9; plt. 31, figs. 9, 10; 1962: 41 - RICKETTS & CALVIN, 1962: 89, and frontispiece (in color) - IW. TAKI, 1964: 409 - BURGHARDT & BURGHARDT, 1969: 22, plt. 2, fig. 28 (in color) - RICE, 1971: 20, plt. 4, fig. 9 (in color) - A. G. SMITH in LIGHT, et al., 3rd ed., 1974: 463, 465 - ABBOTT, 1974: 395, fig. 4639

Diagnosis: Chitons of medium size (up to about 4 cm); color in reddish tones, uniformly, speckled, or with one or two transversal bands of a cream color. End valves and lateral areas with radial rows of robust tubercles defining virtual "ribs" not separated by sulci; central areas with longitudinal riblets cross-ribbed for a latticed effect. Girdle scales convex, often mammillated, obsoletely striated.

Type Material: Lost, or never designated. OLDROYD (1927: 281) stated "Type in Academy, St. Petersburg"; but an inquiry to the Academy of Sciences of the USSR, Leningrad, revealed that "Middendorff's specimens are absent in the Academy collection" (Dr. B. Sirenko, in litt.,

November 12, 1975). Since Middendorff's original specimens cannot be located, a **neotype** specimen from the original locality, Fort Ross, California, is designated, described, and illustrated, in accordance with Article 75 of the International Code of Zoological Nomenclature (ICZN), London, 1964.

The **neotype** is part of a lot of 14 specimens collected intertidally, 800 m south of Fort Ross (38°30.7' N, 123°14.0' W), Sonoma County, California, by Dr. James H. McLean, on December 28, 1963. The **neotype**, partly disarticulated, (LACM 1855), and specimen from the neotype lot (LACM 1856), are placed in the repository of the Los Angeles County Museum of Natural History. Other specimens from the neotype-lot are deposited at the California Academy of Sciences (CASIZ, Type Series no. 701), Zoological Institute of the Academy of Sciences in Leningrad, USSR (no. 1861), Laboratoire de Malacologie, Museum National d'Histoire Naturelle, Paris, and in Iwao Taki Collection, Japan.

Type Locality: "California," as originally given by MIDDENDORFF (1847a). In a subsequent report, MIDDENDORFF (1847b) added "Kalifornien, namentlich die früher Russ. Kolonie Ross. Mertens hatte das Thier dort erbeutet." In view of this statement, the type locality is here restricted to the presently called Fort Ross (38°31' N, 123°14' W), Sonoma County, California.

Original Description: First read publicly on December 11, 1846, but published only on April 20, 1847: "*Chiton testa externa ovali elevata carinata opaca, aspera, fuscocinerea; valva antica valvae ultimae area postica, valvarum denique intermediarum areis lateralibus radiatim expresse granuloscabris. Valvarum intermediarum areis centralibus et valvae ultimae area antica longitudinaliter exsculpte-costatis, costis medianis postica versus dichotomis; costarum interstitia lamellulis erectis transversis in loculamenta dissepita. Valva antica dentibus marginalibus 13 et radiis granuloscabris 26. Valva ultima margine postico convexo dentibus 13 et radiis granuloscabris 20. Valvarum intermediarum radiis granuloscabris quinque. Pallium marginale epidermide fuscocinerea, squamis aspera, obtectum. Squamae hae in series oblique decurrentes ordinatae. Branchiarum series ab initio secundae*

Explanation of Figures 1 to 6

Figure 1: *Lepidozона mertensii*. Neotype (in text), 33.0 mm long (LACM 1855)

Figure 2: *Lepidozона mertensii*. Neotype. Close-up of lateral areas

Figure 3: *Lepidozона cooperi*. 28.2 mm long, Bolinas, California (CASG 30915)

Figure 4: *Lepidozона cooperi*. Close-up of specimen in Figure 3 to show detail of lateral areas

Figure 5: *Lepidozона pectinulata*. 16.3 mm long, San Diego, California (ANSP 118664)

Figure 6: *Lepidozона pectinulata*. Close-up of specimen in Figure 5 to show detail of lateral areas

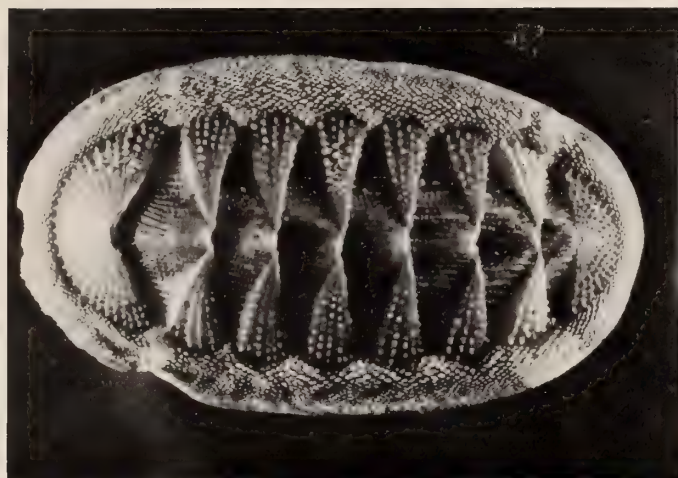


Figure 1



Figure 2

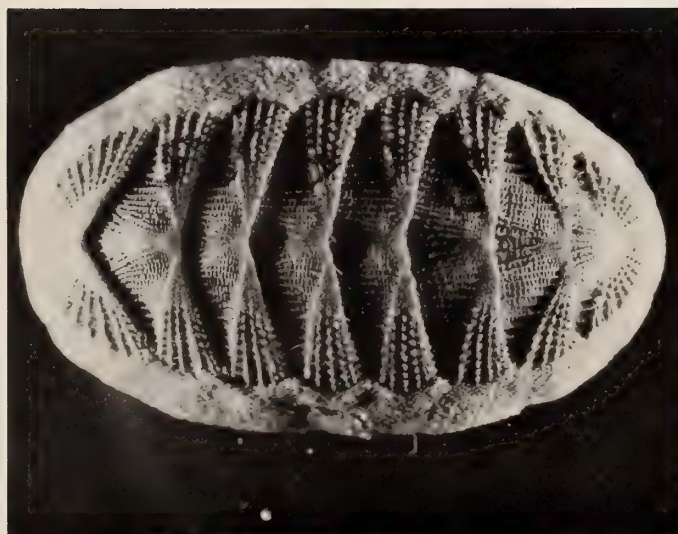


Figure 3

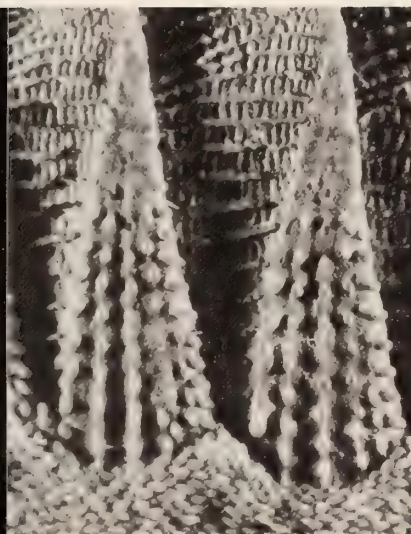


Figure 4

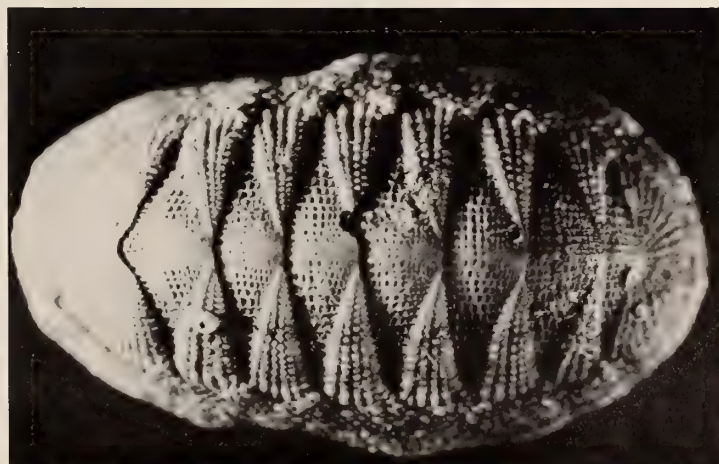


Figure 5



Figure 6

tertia partis totius animalis longitudinis ad vicinitatem ani usque porrecta. Lamellarum branchialium numerus circiter 36. Adulti longitudo 0,23 Decim. Patria: California." (MIDDENDORFF, 1847a: 118).

Description: Neotype (Figures 1, 2) is oval in outline. Shell and girdle are a rather uniform reddish brown with some darker diffused blotches in the pleural areas; 2 wide bands of a creamy-white color cut across the specimen, transversally, at the level of valves ii and vii. The specimen, preserved in ethyl alcohol is perfectly flat; it measures 33.0 mm in length (including girdle), 19.2 mm in width (at the iv level), and 5.2 mm in height. Width/length ratio: 0.58. Jugal angle about 101° .

The tegmentum general surface is minutely granulose. The anterior valve displays some 29 radial rows of very well defined tubercles. The tubercles are round and measure about $250\ \mu\text{m}$ in diameter and height; they are clearly separated from each other by a distance at least as large as their diameter. There are about 7-9 tubercles per radial row; the tubercles towards the top of the valve have fallen off, but their still visible scars indicate that there might have been about 10-11 such tubercles per radial row. On the valve there are no ribs as such; the rows of tubercles define by their presence "ribs" that are only virtual. Otherwise, the surface of the valve is smooth, almost glossy, flat and undivided by sulci or undulations. The intermediate valves, ii to vii, show well defined lateral areas bearing 4-5 similar rows of tubercles disposed in a radial fashion. The central areas display some 14-15, well carved, longitudinal riblets to a side, riblets which tend to diverge forward moderately; between the riblets there is coarse but definite latticing, which becomes obsolete or totally absent towards the jugum. The jugal tract riblets tend to diverge forward, most particularly on valve ii where they outline a wedge-like figure. Posterior valve sculptured in conformity with the other valves. The mucro is central, well defined, but not prominent; the post mucro area is relatively flat except for the presence of about 20 radial rows of tubercles.

The girdle is about 2.5 mm wide, covered with imbricating scales. The scales are strongly convex, and some show a prolongation, nipple, or mammilla, on the dorsal edge [an observation already made by MIDDENDORFF (1847b, plt. fig. 2d), and LOLOUP (1940, fig. 30)]. The scales attain sizes of $450\ \mu\text{m}$ in length. The surface of most scales appears to be smooth or minutely granulose; some occasional scales show very faint, almost obsolete striations.

The articulamentum is white. Sutural laminae are sharp, semioval, relatively short. Sinus is moderately shallow; sinus laminae show a few, irregular pectinations, and are often neatly demarcated from the adjacent sutural

laminae by a small notch. Eaves are solid. Insertion teeth are clean cut, sharp, and relatively short. Slit formula 11-1-11.

The radula measures 13.0 mm in length. Radula relative length (length of radula/length of specimen) is 39%. Number of rows of teeth, 33. The median plate is very wide anteriorly ($400\ \mu\text{m}$) where it displays a thin blade recurved ventrally; medially, the plate narrows rapidly to $100\ \mu\text{m}$ in diameter; posteriorly, it enlarges again into a bulge that resembles two half-joined spheres (Figure 34).

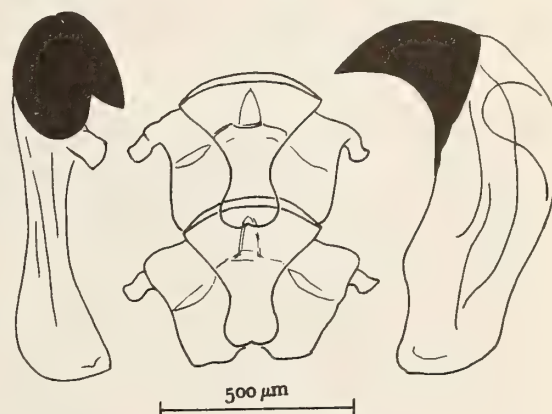


Figure 34

Radula (median, intermediate, and uncinated plates) of the Neotype of *Lepidozона mertensii* (Middendorff, 1847) (camera lucida)

The intermediate plate (first lateral) has a robust recurved knobby growth at each outer-anterior corner. The uncinated (second lateral, major lateral) plate has a unicuspid blade, about $400\ \mu\text{m}$ long. On the inner face of the shaft, immediately underneath the blade, there is a rather thick and long ($200\ \mu\text{m} \times 100\ \mu\text{m}$) tubercle pointing inwardly. This tubercle is obviously very fragile for its presence cannot be demonstrated in but a few teeth; but the fact that it is a normal feature of the *Lepidozона mertensii* radula has been verified many times in other specimens of the same species obtained at the same and other collecting sites.

Scanning electronic micrographs (SEM) of the girdle scales were obtained through the courtesy of Hans Bertsch, Donner Research Laboratory, University of California, Berkeley (Figures 20, 21) from another specimen: The hypotype, dry and flat, measures 26.4 mm in length; it was collected by A. J. Ferreira, on August 4, 1973, at Lovers' Point, Monterey Bay ($36^\circ 37' \text{N}$, $121^\circ 55' \text{W}$), Monterey County, California, in 5 m of water (AJF 56).

Individual Variation: In color, *Lepidozona mertensii* varies appreciably although remaining within the red-orange hues. Within the basic coloration, there are often markings in the form of triangular blotches at the jugum, or dark brown suffusions along the pleural areas, or a peppering of lighter (or darker) specks throughout the tegmentum. Rather characteristic of the species is the presence of one or two transversal bands of a lighter color, creamy-orange to white. When present, the posterior transversal band covers most of the vii valve and adjacent girdle, while the anterior transversal band covers the ii valve and adjacent girdle. Among 83 specimens (7 lots) from Monterey Bay, California, 9 specimens had a single band (on vii), and 11 had a double band. Seemingly the posterior band is much more common than the anterior band for I have never seen a specimen with anterior band without a posterior one. Color does not seem to be correlated to geographic location, depth, or any other recognizable aspect of the habitat.

Individual variation in meristic characteristics is summarized in Table 1, based on a random sample of 20 adult specimens from Monterey Bay, California.

As to size, specimens measuring up to 45 mm in length were found in several lots. Unusually large specimens were collected at Victoria, Vancouver Island, Canada, the largest measuring 51.9 mm in length, 30.8 mm in width, and 10.7 mm in height (Crittenden Colln., leg. S. Crittenden intertidally, June 1970). Specimens above 7 - 8 mm in length were found to display all of the identifying characteristics of the species. The smallest specimens examined, 4 - 5 mm long, already showed the typically convex girdle scales, often faintly striated, but with no mammillation; in contrast with larger ones, these small specimens usually display a spiculate fringe.

Distribution: *Lepidozona mertensii* seems to have a continuous distribution between the parallels 30° N and 58° N, between upper Baja California and Alaska. The northernmost finding in the examined collections is Auke Bay (58° 21' N; 134° 41' W), 24 km NW of Juneau, Alaska (CASIZ, leg. J. E. Bailey, 1 adult specimen, at 25 m). The southernmost finding is Sacramento Reef, just S of Isla San Geronimo (29° 43' N, 115° 45' W), Baja California,

Mexico, 1 specimen at 6 - 12 m (LACM 71-91, leg. J. H. McLean, Sept. 26 - 27, 1971). Two specimens were found at Kellet Channel, south of Cedros Id. (27° 57' N, 115° 08' W), Baja California, Mexico (LACM 71-159, leg. J. H. McLean & P. LaFollette, *R/V Searcher*, Oct. 20, 1971), sizes 18 and 9 mm in length, and another specimen, 7 mm long, found at the southern tip of Natividad Island (27° 52' N, 115° 11' W), Baja California, Mexico, (LACM 72-116, leg. J. H. McLean, Sept. 25, 1972); but they were referred to *L. mertensii* only tentatively, their small size, and a few ambiguous features precluding a positive identification.

Between these two extreme points, *Lepidozona mertensii* was found often abundantly in many other collecting stations, including the offshore islands of San Geronimo (LACM 71-91), San Nicolas (LACM 72-100), Catalina (LACM 65-6), Santa Cruz (LACM 63-5), San Miguel (LACM 67-38), Farallon (LACM 62-9), San Juan (CASIZ-AGS 10097; CASG 18058; LACM 66-39), Vancouver (LACM 63-31, 63-32, 73-35, 73-38, 73-39, 73-40), Queen Charlotte (LACM 69-52), Baranof (CASG 43941; LACM 73-13, 73-15, 73-16), Kosciusko (CASIZ 32430), Dall (CASG 32433, 32564), Forrester (SDNH 23436; UCLA 22317).

The recorded depth range of *Lepidozona mertensii* extends from the intertidal zone to about 100 m (CASG 32536, 36334 off San Pedro; CASG 24147, Monterey Bay, California).

Lepidozona mertensii has been reported in northern Japan, at Hakodate and Mutsu Bay (Is. TAKI, 1938: 390-393; 1962: 41).

Remarks: The presence of *Lepidozona mertensii* at Guadalupe Island, Mexico, as reported by CHACE (1958) and A. G. SMITH (1963), must be considered as misidentifications for the rather similar *Lepidozona guadalupensis* Ferreira (herein), as concluded from the examination of the material collected at Guadalupe Island by M. Woodbridge Williams, in July 1946 (CASIZ G-32746), by C. L. Hubbs *et al.* (SDNH 9957), and recently by Welton L. Lee & A. J. Ferreira (AJF 210-211). To my knowledge, *Lepidozona mertensii* has not been collected at Guadalupe Island.

Explanation of Figures 7 to 12

Figure 7: *Lepidozona scabricostata*. 14.5 mm long, Cordell Banks, California (CASG 43983)

Figure 8: *Lepidozona scabricostata*. Close-up of specimen in Figure 7 to show detail of lateral areas

Figure 9: *Lepidozona willetti*. Paratype (CASG 1123)

Figure 10: *Lepidozona willetti*. Close-up of specimen in Figure 9 to show detail of lateral areas

Figure 11: *Lepidozona retiporosa*. Topotype, 13.0 mm long (CASG 43840)

Figure 12: *Lepidozona retiporosa*. Close-up of specimen in Figure 11 to show detail of lateral areas



Figure 7



Figure 8

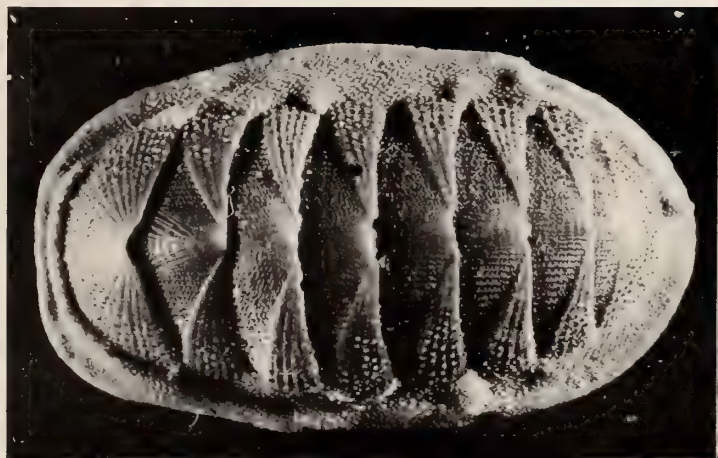


Figure 9

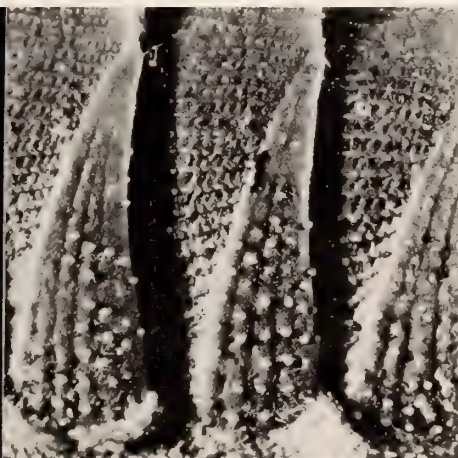


Figure 10

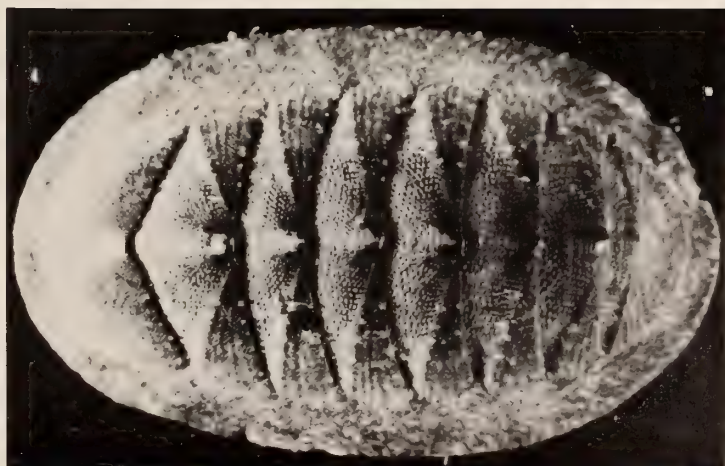


Figure 11

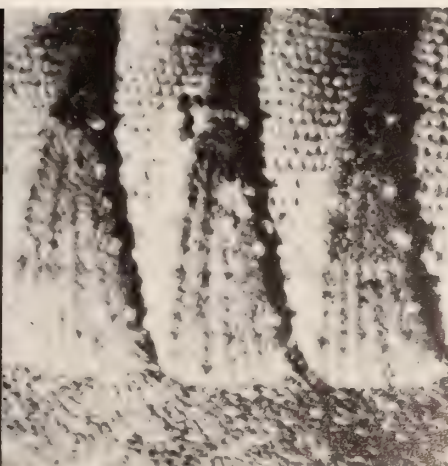


Figure 12

Lepidozona cooperi (Dall, 1879)

(Figures 3, 4, 22, 23)

Ischnochiton cooperi DALL, 1879, 1: 296, fig. 15 (radula); WOOD & RAYMOND, 1891, 5: 58; PILSBRY, 1892, 14: 127, plt. 26, figs. 27-30 (in section *Lepidozona*); 1898, 50: 288; HEATH, 1904, 56: 257; 1905, 29 (12): 391-392; BERRY, 1907, 21 (5): 51; PACKARD, 1918, 14 (2): 293-294; CHACE & CHACE, 1919, 2 (6): 3 (fossil); 1933, 46 (4): 124; DALL, 1921, 112: 192 (in section *Lepidozona*); OLDROYD, 1927, 2 (3): 281 (in section *Lepidozona*); JOHNSON & SNOOK, 1927: 564, fig. 670; SIMROTH & HOFFMANN, 1929: 314; STOHLER, 1930, 91 (5/8): 151, 155; LELOUP, 1940: 12-15, figs. 34-37; RICKETTS & CALVIN, 1962: 89, 453, plt. 19, fig. 4

Ischnoplax cooperi, THIELE, 1893, 2: 376, plt. 31, fig. 2 (radula)

Ischnochiton (Lepidozona) cooperi, BERRY, 1922, 11: 473, plt. 11, figs. 1-12 (fossil); A. G. SMITH, 1947: 18; A. G. SMITH & GORDON, 1948, 26: 207; PALMER, 1958: 273-274, plt. 34, figs. 1-6

Lepidozona cooperi, BURGHARDT & BURGHARDT, 1969a, 12 (2): 228; 1969b, 21, plt. 2, fig. 27 (in color); RICE, 1971: 20, plt. 4, fig. 10 (in color); ABBOTT, 1974: 395, fig. 4641; A. G. SMITH in LIGHT's, 3rd ed., 1974: 463, 465, plt. 109, fig. 5

Ischnochiton cooperi acutior Carpenter in DALL, 1919, 55 (2283): 508; DALL, 1921, 112: 192 (in section *Lepidozona*); OLDROYD, 1927, 2 (3): 282; WILLET, 1935, 49 (2): 44; PALMER, 1945, 58 (3): 101; 1958: 274, plt. 34, fig. 16 (synonymized with *I. cooperi*); A. G. SMITH, 1977, 19 (3): 222-223 (synonymized with *Lepidozona cooperi*)

Nomenclatural Comments: The name *Ischnochiton cooperi* was first published by DALL (1879) who attributed it to Carpenter whose unpublished manuscript he had been "authorized to use" (DALL, *l.c.*: 282). Dall limited himself to describe and figure the radula; but from all appearances the description was his own, not Carpenter's, as revealed through the examination of the pertinent pages in Carpenter's manuscript made available to me through the courtesy of Dr. Joseph Rosewater, National Museum of Natural History, Washington, D.C. Manuscript names having no standing in taxonomy, Dall's published account, an "indication" in the sense of Articles 16, 17 and 24.b of the International Code of Zoological Nomenclature (ICZN), clearly establishes the authorship of the species as Dall's.

The synonymy of *Ischnochiton cooperi acutior* Carpenter in Dall, 1919, was suggested by Dall himself with the comment that "the only differences from *I. cooperi* I could perceive were that the specimens of the variety *acutior* were lighter in color, more emphatic in sculpture . . . In a group where color is often without systematic value, these differences seem hardly worthy a name . . ." (DALL, 1919: 508). From the examination of the holotype (USNM

30734), A. G. SMITH (1977: 223) concluded "that *Lepidozona cooperi acutior* merely represents a young phase of *L. cooperi* . . ."; the study of A. G. Smith's color slide of the holotype (CASIZ, Color Slide Series No. 2048) led me to the same conclusion. The synonymy of *acutior* had also been suggested by PALMER (1958: 274) upon the examination of specimens labelled "types" in the Carpenter Collection at the Redpath Museum, Montreal, Canada. However, a curious fact must be noted here: Although the 5 specimen-lot from Todos Santos Bay (Redpath Museum no. 18) figured in PALMER (1958: plt. 34, figs. 1-5) are unquestionably *Lepidozona cooperi*, the lot of 6 specimens from "near S. Diego" (Redpath Museum no. 8) is not correctly identified. Despite being accompanied by a characteristic Carpenter label of white ink on glass which reads "*Ischnochiton cooperi*, var. *acutior*," and having been regarded and photographed as such by PALMER (1958: plt. 34, fig. 6), all 6 specimens in the Redpath Museum no. 8, examined on a loan through the courtesy of Dr. Vincent Condé, Redpath Museum, are of *Lepidozona sinudentata* (Carpenter in Pilsbry, 1892).

Diagnosis: Chitons of medium size (up to 4 cm), uniform color of greenish, gray, or brown tones. End valves and lateral areas with rows of strong tubercles on radial ribs separated by well defined sulci. Central areas with longitudinal riblets, cross-ribbed. Articulamentum blue. Girdle scales convex, oval, with deep striations.

Type Material: "No specimens have been found which could be identified as type for Dall's description" (PALMER, 1958: 273). Since further search for Dall's original material proved fruitless, a neotype specimen is here designated and illustrated in accordance with Article 75 of ICZN (London, 1964). The specimen chosen as neotype is part of a lot of 8 specimens collected by myself (AJF 149) at Cayucos (35°27'N, 120°54'W), San Luis Obispo County, California, intertidally, on April 11, 1974. The neotype (partly disarticulated) and its radula are in repository at the California Academy of Sciences, Department of Geology (CASIZ, Type Series No. 702). Specimens from the neotype-lot are deposited at the Los Angeles County Museum of Natural History (LACM 1858), National Museum of Natural History (USNM 770961), and Academy of Natural Sciences of Philadelphia (ANSP 344915).

The holotype of *Ischnochiton cooperi acutior* is at the National Museum of Natural History (USNM 30734).

Type Locality: Cayucos (35°27'N, 120°54'W) San Luis Obispo County, California. The locality of Dall's specimen is unknown (PALMER, 1958: 273).

Description: DALL (1879: 266; fig. 15) only described and figured the radula. The earliest full description of the species comes from PILSBRY (1892, 14: 127; figs. 27-30) whose material [ANSP 118659] has been regarded as "typical" by some authors.

The neotype is oval and somewhat carinated. The color is a uniform dingy gray. Dried, but fully extended, it measures 36.8 mm in length, 21.5 mm in width, and 7.0 mm in height. Width to length ratio: 0.58. Jugal angle about 96°.

The anterior valve displays about 20 poorly differentiated radial ribs which show a tendency to twin towards the periphery. The ribs are crested by well formed tubercles, oblong rather than round, which show a tendency to become confluent. On average the tubercles measure 0.3 mm in diameter; there are about 15 tubercles on each rib. The posterior valve shows, in the post mucro area, a similar sculpture of some 20 radial ribs crowned by a row of tubercles; the mucro is central, well defined but not conspicuous. The lateral areas of the intermediate valves bear 4-6 tuberculated ribs, also with a tendency to bifurcate towards the periphery. The central areas have about 18-20 longitudinal riblets per side, neatly cross-ribbed for a definite lattice effect. The jugal tract has only vestigial cross-ribbing; it has a tendency to diverge forward, particularly on valve ii where the riblets outline a wedge-like figure.

The articulamentum is light blue in color. Sutural laminae are sharp, semioval, and separated by a relatively shallow sinus. Sinus laminae are irregularly pectinated, and separated from the adjacent sutural laminae by a small notch. Eaves are solid. Teeth are sharp-edged, clean-cut, and straight. Slit formula 10-1-11.

The girdle is about 2.5 mm wide, covered with imbricating oval scales. The scales are moderately convex, and display some well marked undulations, 8-10 per scale, which define that many ribs and striations. The largest scales average 360 µm in length.

The radula measures 13.2 mm in length, and has 34 rows of mature teeth. The relative length of the radula is 36%. The median plate is wide anteriorly (330 µm), then narrows rapidly in its middle part (100 µm) to bulge again posteriorly in a sort of spheroid; from its anterior edge, a thin blade curves ventrally. The intermediate plate has a strong, knobby growth in the outer-anterior corner. The uncinated plate has a long (450 µm) unicuspid blade on a shaft about 700 µm long. A thick and long tubercle in the upper part of the uncinated plate points inwardly.

The specimen in the photograph (Figure 3, 4), measures dried, but fully extended, 28.2 mm in length, 17.3 mm in width, and 6.8 mm in height. It is part of a lot of 5 specimens collected at Bolinas, Marin County, California (CASG 30915).

The specimen used for the SEM micrographs of the girdle scales (Figures 22, 23), measures 30 mm in length, and was collected at Point St. George, Del Norte County, California (CASG 53072).

Individual Variation: *Lepidozona cooperi* varies little in color, staying within the range of dark browns, greens, or grays, for an overall dingy, inconspicuous appearance. Variation in meristic characteristics are summarized in Table 1. In size, only a few specimens examined were longer than 40 mm. The largest specimen seen measures 44.5 mm (SDNH 53812, Crescent City, California). Specimens as small as 5 mm already show identifying characteristics, particularly the distinctive girdle scales.

Distribution: The known range of *Lepidozona cooperi* extends from latitude 32° N to 48° N. The northernmost record is Neah Bay (48° 22' N; 124° 37' W), at the entrance of the Strait of Juan de Fuca, Washington (RICE, 1971). The southernmost locality is Puerto Santo Tomas (31° 34' N; 116° 40' W), Baja California, Mexico (LACM 67-2, leg. J. H. McLean, Jan. 8-10, 1967). The species has been recorded, too, from Catalina (DALL, 1921), and Sta. Cruz Islands (AJF, Dec. 1970) on the outer coast of California.

Explanation of Figures 13 to 19

Figure 13: *Lepidozona guadalupensis* Ferreira, spec. nov. Paratype 13.0 mm long (LACM 1857)

Figure 14: *Lepidozona guadalupensis* Ferreira, spec. nov. Close-up of specimen in Figure 13 to show detail of lateral areas

Figure 15: *Lepidozona sinudentata*. Topotype, 15.0 mm long, Monterey Bay, California (AJF 89)

Figure 16: *Lepidozona sinudentata*. Close-up of specimen in Figure 15 to show detail of lateral areas

Figure 17: *Lepidozona sinudentata*. 17.5 mm long specimen from Todos Santos Bay, Baja California, Mexico, ex G. Willett collection (UCLA 22382). Close-up of lateral areas

Figure 18: *Lepidozona sinudentata*. 11 mm long specimen from San Diego, California (CASG 40837). Close-up of lateral areas

Figure 19: *Lepidozona sinudentata*. 12 mm long specimen from Carmel Bay, California (CASG 53074): scales on the underside of the girdle approximately × 300

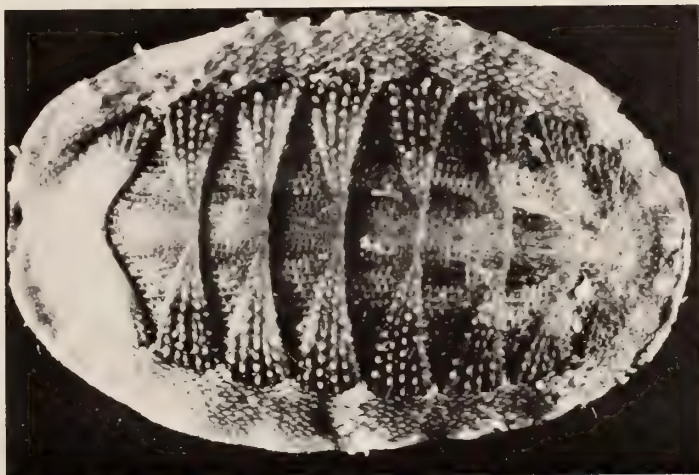


Figure 13

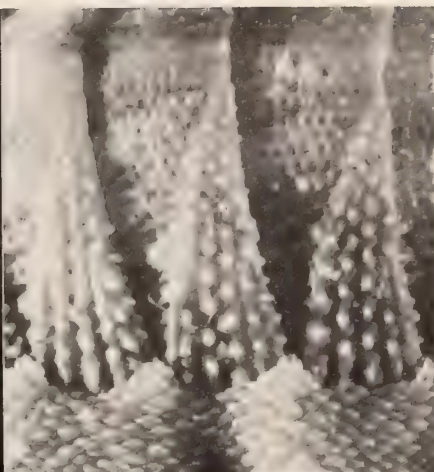


Figure 14



Figure 15

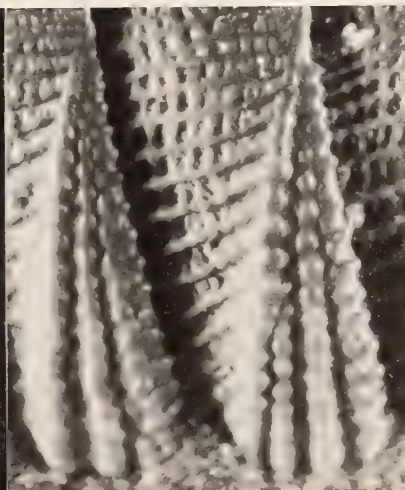


Figure 16



Figure 17

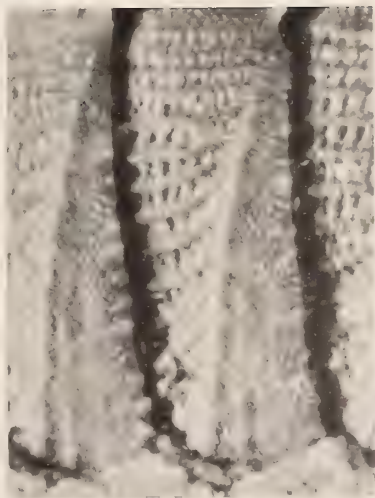


Figure 18



Figure 19

The known depth range is from intertidal to about 20 meters.

Remarks: In size, shape, and valve sculpture, *Lepidozonia cooperi* is rather close to *L. mertensii*. The main distinguishing features are in the tuberculated radial ribs, the color of the articulamentum, and the very decidedly different girdle scales. To a considerable extent, the two species share range and habitat, although *L. cooperi* seems to favor shallower depths than *L. mertensii*. In general appearance, size, and coloration, *L. cooperi* is remarkably similar to *Lepidozonia coreanica* (Reeve, 1847) from Japan; the two species may be regarded as cognates, the differences in sculpture being rather subtle and difficult to pinpoint except for the distinctive, though similar, girdle scales.

Lepidozonia pectinulata (Carpenter in Pilsbry, 1893)

(Figures 5, 6, 28)

- Ischnochiton (Lepidopleurus) pectinatus* CARPENTER, 1864a: 612 (Reprinted, 1872: 98), *nomen nudum* [not *Chiton pectinatus* Sowerby, 1840]; 1866, ser. 1, 3: 211 - 212
- Lepidopleurus pectinatus* CARPENTER, 1864b: 649 (Reprinted, 1872: 135) [= *Ischnochiton cooperi* Carpenter in Dall, 1879, in part, *fide* PILSBRY, 1893, 14: 129] - COOPER, 1867: 22; 1870: 59
- Ischnoplax pectinatus*, KEEP, 1887: 112 (Reprinted, 1888, 1891, & 1893)
- "*Chiton (Lepidopleurus ?) pectinulatus* Cpr.", DALL in ORCUTT, 1885: 544, *nomen nudum*
- Lepidopleurus pectinulatus* Carpenter in MS, PILSBRY, 1893, 14: 129 [syn. of *Ischnochiton clathratus* (Reeve, 1847) in part]
- Ischnochiton pectinulatus*, BERRY, 1922: 412, 414, 421, tbl. 1 (fossil)
- Ischnochiton (Lepidozonia) pectinulatus*, BERRY, 1922: 471 - 472, plt. 10, figs. 4 - 6
- "*Ischnochiton punctulatissimus* Carpenter", LOWE, 1904: 19 [? error for *I. pectinulatus*]
- Ischnochiton clathratus* (Reeve, 1847), PILSBRY, 1892 - 1893, 14: 128 - 129 (in part); KEEP, 1904: 349; BERRY, 1907: 51; CHACE, 1917: 30 (fossil) [= *I. (Lepidozonia) sanctaemonicae* Berry, 1922, *fide* BERRY, 1922: 471, footnote]; OLDROYD, 1924: 193; 1927: 282; LELOUP, 1940: 3, 15 - 18; figs. 38 - 41
- Ischnochiton (Ischnochiton) clathratus* (Reeve, 1847), DALL, 1921: 192 (in section *Lepidozonia*)
- Lepidozonia pectinulata*, FERREIRA, 1974: 165; A. G. SMITH, 1977: 216, 229 - 231
- Ischnochiton bryanti* DALL, 1919: 503; 1921: 190; A. G. SMITH, 1947: 18; BURGHARDT & BURGHARDT, 1969: 16 (syn. of *I. brunneus* Dall, 1919); ABBOTT, 1974: 395
- Ischnochiton brunneus* DALL, 1919: 504; 1921: 190; OLDROYD, 1927: 271; A. G. SMITH, 1947: 18; BURGHARDT & BURGHARDT, 1969: 16 (with syn. *I. bryanti* Dall, 1919); ABBOTT, 1974: 395

Ischnochiton (Lepidozonia) californiensis BERRY, 1931: 255 - 258, plts. 29, figs. 1 - 2; A. G. SMITH, 1947: 18; A. G. SMITH & GORDON, 1948, (4) 26 (8): 207; PALMER, 1958: 272 - 273; plt. 31, figs. 5, 6

Ischnochiton californiensis, THORPE, 1962: 205

Lepidozonia californiensis, A. G. SMITH, 1960: 56; fig. 38, 8 (fossil); McLEAN, 1969: 64; fig. 35.5; BURGHARDT & BURGHARDT, 1969: 20, 43, plt. 2, fig. 26 (in color); PHILLIPS, 1971: 22; ABBOTT, 1974: 395

Nomenclatural Comments: CARPENTER (1864b: 612) introduced *Ischnochiton (Lepidopleurus) pectinatus* without a description. The *nomen nudum* situation was soon remedied when Carpenter provided a short description of the species (1864b: 649), and a full description later (1866, 3: 211 - 212). According to PILSBRY (1893, 14: 129), Carpenter's first description of *Lepidopleurus pectinatus* [so inadequate that it is impossible to say to what taxon it would apply] referred to "*I. cooperi*, Cpr."; and the second, much fuller description of the species (1866) "seems to have included both this species [*Ischnochiton clathratus* (Reeve, 1847), *sensu* PILSBRY, 1893] and *I. cooperi*." However, afterwards, "upon receipt of better material," Carpenter distinguished *I. cooperi* from *I. pectinatus*, and [in the realization that the name "*pectinatus*" was preoccupied by *Chiton pectinatus* Sowerby, 1840] re-named the latter *pectinulatus*.

Nomenclatural difficulties might have been minimal at this point were it not for Pilsbry's misunderstanding of *Chiton clathratus* Reeve, 1847, as the "species that seems to replace *I. mertensii* south of Monterey . . . a dingy, lusterless shell resembling *mertensii* in the shape of the girdle scales . . ." (PILSBRY, 1893: 129), and, as such, senior synonym of *I. pectinulatus* Carpenter in MS.

The misunderstanding so created was not unraveled until BERRY (1931) pointed out that Pilsbry's interpretation of *Chiton clathratus* Reeve, included two distinct species, *Lepidozonia clathrata* (Reeve, 1847) confined to the Gulf of California, Mexico, and "the commonest southern California *Lepidozonia*" to which old collectors [like Henry Hemphill (A. G. SMITH, 1977: 230)], and authors [like BERRY himself (1922)] had referred to as "*pectinulatus*."

However, BERRY (1931) reached the conclusion that Carpenter's "*pectinulatus*" was not a valid name for the southern California species since it had been first published (PILSBRY, 1893) in synonymy, a fact which, by the old *Règles* (1905) [in a rule not changed until the ICZN of 1963], made it unavailable for purposes of nomenclature. In this frame of opinion, Berry concluded that the southern California species had been left without a valid name, and proceeded to rename it *Ischnochiton (Lepidozonia) californiensis* Berry, 1931.

It now seems that Berry's new name for the species was unnecessary for the following reason: 1) Carpenter's second description (1866) of *Ischnochiton* (*Lepidopleurus*) *pectinatus* is quite adequate and explicit even by present standards, 2) the existence of a syntype series (Redpath Museum no. 70) of *I. pectinatus* labeled by Carpenter as "type" (photographed in PALMER, 1958: plt. 31, figs. 5, 6) [not mentioned in either PILSBRY, 1893, or BERRY, 1931], and 3) the fact that the name "*pectinulatus*" was clearly validated by PILSBRY (1893: 129) as replacement for "*pectinatus*." Meanwhile, Berry's objections to the use of the name "*pectinulatus*" were further weakened in 1963 when the ICZN modified the rule 11(d) to allow the use of such names in synonymy if, before 1961, they had been treated as available names. It is ironical to observe that BERRY (1922) himself clearly used *L. pectinulata* as an available name, thus unwittingly providing the basis for invalidating his new name "*californiensis*."

In this respect, some unpublished notes left by Pilsbry [conveyed to Allyn G. Smith (personal communication) through R. Tucker Abbott, then with the Academy of Natural Sciences of Philadelphia] and clearly intended for publication, are of historical interest. With the kind permission of Dr. Robert Robertson (*in litt.*, 22 October, 1973), I quote from Pilsbry's notes on the subject of "*Lepidopleurus pectinulatus* Cpr. MS": "... Carpenter had formerly called the southern California shell '*L. pectinatus*' (not of Sowerby) though this is known by specimens he labeled rather than by his inadequate definition. I stated (p. 129) [Manual of Conchology, 1893, vol. 14] that he had 'renamed the present form *pectinulatus*'. The 'present form' referred to being that I had just described [*C. clathratus* Reeve]. My description and figures were from Californian specimens... My definition did not 'include both Panamic and Californian races' as stated by Dr. Berry... I, as it now appears erroneously, considered Reeve's unlocalized *C. clathratus* to be the Californian species... The Californian species was already commonly known under the name *pectinulatus* when I wrote the monograph... There seems to be no necessity for giving a new name in view of the treatment of the form in the Manual of Conchology. It should stand as *Ischnochiton* (*Lepidozona*) *pectinulata* ("Cpr.") Pils... with the synonymy as given by Berry (1931: 255) to which is to be

added *I. (L.) californiensis* Berry, l.c. . . . a name which appears to me to be superfluous." Pilsbry's belated conclusions are supported by the finding of two lots of specimens in the Type Collection of the Academy of Natural Sciences of Philadelphia associated with the name *pectinulatus*. One (ANSP 118664) consists of 13 specimens accompanied by three labels which, combined, read: "*Lepidopleurus pectinulatus* Cpr.; San Diego, California; collected by Henry Hemphill; on rocks between tides; Type, figs. 31 - 33" [the statement "Type, figs. 31 - 33" obviously refers to Pilsbry's monograph in Tryon's Manual of Conchology, 1892 - 1893, vol. 14; and together with the identification *I. pectinulatus* Cpr., it is lettered in ink, likely by Pilsbry himself (SMITH, 1977: 230)]. The second lot (ANSP 118662), consists of two specimens; the label reads "*L. pectinatus* Cpr./*I. clathratus* Rv. . . ." the name "*clathratus*" had been crossed out, and the name "*californiensis*" written in pencil over the name "*pectinatus*"; to the right of the card on which the larger specimen seems to have been mounted, a pen-written "2nd measurement/M.C. p. 128" suggests that the specimen was used for one of the measurements published in the Manual of Conchology (SMITH, 1977: 229). The specimens in both lots, available through the generosity of Dr. Robert Robertson, Academy of Natural Sciences of Philadelphia, are unquestionably conspecific with *Ischnochiton* (*Lepidozona*) *californiensis* Berry, 1931, and with Carpenter's syntype series of *I. pectinatus* at the Redpath Museum.

It is interesting to note that prior to Pilsbry's monograph, the name "*pectinulatus* Cpr." had already been introduced in the literature, albeit as a *nomen nudum*, by DALL (*in* ORCUTT, 1885) who had been working from Carpenter's MS, presumably the same MS used by Pilsbry.

From the marshalling of all the evidence, it seems appropriate to call the species in question *Lepidozona pectinulata* (Carpenter in Pilsbry, 1893), and so bring the whole taxonomic problem to rest.

The synonymization of *Ischnochiton brunneus* Dall, 1919, and *Ischnochiton bryanti* Dall, 1919, is based upon Dall's original descriptions, and the examination of the respective holotypes made available through the kindness of Dr. Joseph Rosewater, United States Museum of Natural History, Washington, D.C.

Explanation of Figures 20 to 27

Figure 20: *Lepidozona mertensii*. Girdle scales. approx. $\times 240$
 Figure 21: *Lepidozona mertensii*. Girdle scales. approx. $\times 100$
 Figure 22: *Lepidozona cooperi*. Girdle scales. approx. $\times 300$
 Figure 23: *Lepidozona cooperi*. Girdle scales. approx. $\times 100$

Figure 24: *Lepidozona scabricostata*. Girdle scales. approx. $\times 300$
 Figure 25: *Lepidozona scabricostata*. Girdle scales. approx. $\times 60$
 Figure 26: *Lepidozona retiporosa*. Girdle scales. approx. $\times 650$
 Figure 27: *Lepidozona retiporosa*. Girdle scales. approx. $\times 400$

SEM micrographs by Hans Bertsch



Figure 20



Figure 22



Figure 21



Figure 23



Figure 24

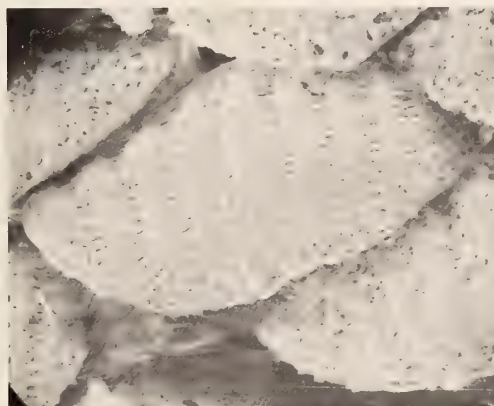


Figure 26



Figure 25

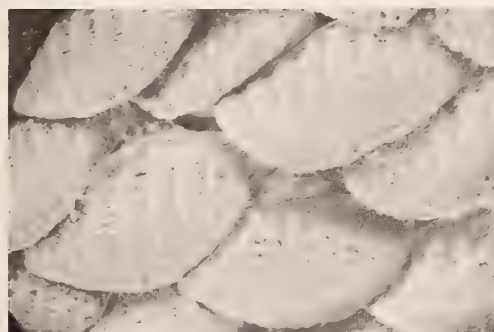


Figure 27

Type Material: "There are in the Redpath Museum two complete specimens and three separate plates which were labelled by Carpenter, 'Type La Paz Pease'" (PALMER, 1958: 273). Although the locality of the specimens must be in error, the specimens must be regarded as a syntype series. The one specimen figured in PALMER (1958: plt. 31, figs. 5, 6), whose dimensions are given as 25×10 mm, is here designated as **lectotype**; the other two in the lot as **paralectotypes** (Redpath Museum No. 70).

Ischnochiton (Lepidozona) californiensis Berry, 1931: Holotype in Berry Colln. (Cat. No. 5226). Paratypes in Berry Colln. (Cat. No. 3119), SDNH, ANSP, USNM, British Museum (Natural History), and Stanford University (Department of Geology). Color slides of paratype (ANSP 161525) at CASIZ, Color Slide Series Nos. 2968 - 2969 (A. G. Smith).

Ischnochiton brunneus Dall, 1919: Holotype (USNM 58734a). Color slides at CASIZ, Nos. 2972 - 2973 (A. G. Smith), and Nos. 3107 - 3108 (AJF).

Ischnochiton bryanti Dall, 1919: Holotype (USNM 253826). Color slides at CASIZ, Nos. 2965 (A. G. Smith), and No. 3109 (AJF).

Diagnosis: Chitons of medium size (up to about 4 cm), uniformly colored mostly in tones of muddy brown to orange. End valves and lateral areas of intermediate valves with strongly granular radial ribs. Central areas with longitudinal riblets, clearly cross-ribbed. Girdle scales imbricated, strongly convex, faintly striated, and mammillated.

Type Locality: As mentioned above, the locality attributed to the syntypes must be in error. The first specimen reported as *I. pectinatus* Carpenter (1864a: 612), a *nomen nudum*, was from Catalina Island, California. The second reference (1864a: 649) mentioned specimens from Santa Barbara Islands. Carpenter's 1866 description lists Catalina and Santa Barbara Islands. The type locality is here restricted to Catalina Island, California.

Original Descriptions: "Olive, strong sculpture over shagreened surface: side areas ribbed; outer margin and inner sutures pectinated. Bch." (Carpenter, 1864a: 649).

"State Collection, No. 1073. *L.t.'L. Mertensii* simili, sed omino olivaceo; areis diagonalibus radiis plerumque iv. dense tuberculiferis, radioque altero suturali tuberculis inflexis, margines valvarum pectinantibus; costis transversis crebris validis; costulis longitudinalibus acutis distantibus superantibus, quarum margines suturas anticlas pectinant; valv. term. ut in areis diag. sculptis, seriebus tuberculorum creberrimis; tota superficie minutissime tuberculata: intus, valvis centralibus unifissatis, terminalibus xi-xv-fissatis: scalis pallii irregularibus, confertis, minutissime longitudinaliter striatis. Long. 0.85, lat. 0.50,

div. 110° . Variat: *interdum aurantio nebulosa*. Hab. Catalina Island, Santa Barbara Island, beach, Cooper." (Carpenter, 1866: 211 - 212).

Description: The splendid account of *Lepidozona californiensis* given by BERRY (1931) is amply sufficient for the understanding of *Lepidozona pectinulata*. The following observations are to be taken only as a supplement to, not an improvement upon that account.

The specimen studied (ANSP 118664, leg. H. Hemphill, San Diego, Calif.), is of a uniform dark muddy brown color (Figures 5, 6). Dried, but perfectly flat, it measures (including girdle) 27.0 mm in length, 16.3 mm in width, and 5.5 mm in height. Width/length ratio: 0.60. Jugal angle about 99° . Anterior valve shows about 24 radial ribs, some twinning towards the periphery. The ribs are composed of a series of granules (about 15 per rib), round, close-packed; each granule is separated from the ones above and below on the rib by a space about half as wide as the granules themselves. The space between the ribs is well defined, distinct, and about as wide as the granules. Posterior valve has some 20 similar granular radial ribs; mucro is low, and inconspicuous. Post-mucro area slightly concave. In the intermediate valves, the lateral areas have about 5 similar granular ribs; the granules in the posterior rib tend to be elongated in the antero-posterior direction, protruding posteriorly and so conferring on the posterior edge of the lateral area a serrated appearance. Central areas with longitudinal riblets (about 15 per side), with equally well developed cross-riblets which results in a marked clathrate appearance of square pits. The jugal riblets diverge forward on valve ii forming a wedge-like figure; similar, but less accentuated divergence of the jugal riblets is also seen on valve iii. The space between the longitudinal riblets at the jugum is smooth, not cross-ribbed. The girdle scales are large (up to 400 μ m), strongly convex, faintly striated. A nipple-like prolongation is observed at the dorsal edge of many of the scales, particularly on the larger ones closer to the valves; the nipple tends to be elongated along the edge, looking more like a crest than a nipple.

The soft parts of the animal had been removed. The articulamentum is bluish white. Sutural laminae are semi-oval, moderate in size. Sinus is relatively shallow; the sinusal laminae show a few irregular pectinations and, in some, there was a small notch separating them from the adjacent sutural laminae. Teeth, eaves, and slit formula not determined.

Color slides of the specimen at CASIZ Color Slide Series Nos. 3118 - 3119 (AJF).

Another specimen (CASG 43928, San Diego, shore, California, coll. T. S. Oldroyd, ex M. Gordon Colln.), was

used for SEM microphotographs of the girdle scales (Figure 28); the specimen measures 28 mm in length; it was the largest in a lot of 27.

A specimen from near the type locality (AJF 148, Bird Rock, La Jolla, San Diego County, California, leg. A. J. Ferreira, intertidally, April 10, 1974), measuring 25.0 mm in length (including girdle) was used for further examination: The eaves were solid, the slit formula was 11 - 1 - 12.

The radula of this specimen measures 11.2 mm in length, and it has 42 rows of teeth. Radula relative length, 48%. The median plate is wide anteriorly (280 μ m) where it sports a small ventrally recurved blade; the plate narrows medially (to 100 μ m) and ends posteriorly in a bulging spheroid, about 140 μ m in diameter. The intermediate plate bears a knobby growth at the outer anterior corner. The uncinated plate is unicuspid, the blade being about 280 μ m in length, on a shaft about 550 μ m long. On the upper part of the shaft a thick, blunt tubercle protrudes inwardly, although only visible on a few plates.

Individual Variation: Color variations of *Lepidozona pectinulata* stay within rather narrow limits, from a uniform dark muddy brown to orange. Some occasional specimen shows a wide and ill-defined band of a lighter coloration of orange running longitudinally across the pleural and lateral areas. In size, *L. pectinulata* does not usually exceed 35 mm in length; the largest specimen examined measures 40 mm in length (CASG, San Diego, California, ex H. Hemphill Colln.). Variation in the number of radial ribs, slit formula, etc. is summarized in Table 1, based upon a random sample of 20 adult specimens.

Distribution: *Lepidozona pectinulata* seems to be confined to the San Diego Province, within the parallels 24° N and 35° N. The distribution seems to be continuous, and includes the offshore islands, with findings at Catalina Island (SDNH 57716; CASG 4055; LACM 64-26 & 71-99), San Clemente Island (SDNH 53814; LACM 66-51), San Geronimo Island (LACM 67-62), Sacramento Reef (AJF 94; LACM 71-91), San Martin Island (LACM 68-31), Navidad Island (LACM 72-116) and Cedros Island (SDNH 60709; LACM 67-65 & 71-92). Its northernmost record is Cayucos (35° 27' N, 120° 54' W) San Luis Obispo County, California (CASG 13784, H. Hemphill Colln.); the southernmost record is NW side of Santa Margarita Island (24° 31' N, 111° 57' W), Magdalena Bay, Baja California, Mexico (LACM 67-73, intertidal, leg. J. H. McLean, Dwyer Expedition, December 15, 1967). Bathymetrically, *L. pectinulata* has been collected from intertidal to about 20 m (LACM 72-115, 50 - 65 feet, S side Piedra Colorada, SW tip Cedros Island, Baja California, Mexico, leg. J. H. McLean, September 24, 1972).

Remarks: The relative allopatry between *Lepidozona pectinulata* and *L. mertensii* has been noticed since the days of PILSBRY (1893: 129). In relation to the species of *Lepidozona* in the Gulf of California it is worth pointing out that *L. pectinulata* has decided affinity not only to *L. clathratus* (Reeve, 1847) with which it was long confused, but to *L. formosa* Ferreira, 1974 as well.

Lepidozona sinudentata (Carpenter in Pilsbry, 1892)

(Figures 15, 16, 17, 18, 19, 29)

- Ischnochiton (Ischnochiton) sinudentatus* Carpenter MS in PILSBRY, 1892, 14: 128 (in section *Lepidozona*); DALL, 1921: 192 (in section *Lepidozona*); OLDROYD, 1927: 283 (in section *Lepidozona*); A. G. SMITH, 1977: 216, 235 - 236
- Ischnochiton (decipiens* var. ?) *sinudentatus*, PILSBRY, 1898: 288
- Ischnochiton sinudentatus*, KEEF, 1904: 349; BURCH, 1942: 7; PALMER, 1945: 101; LIGHT's Manual, 2nd ed., 1954: 217, 219
- Ischnochiton (Lepidozona) sinudentatus*, BERRY, 1922: 476 - 477, tbl. 1, plt. 12, figs. 10 - 17; PALMER, 1958: 276, plt. 30, figs. 8, 9; plt. 33, figs. 1 - 5; A. G. SMITH, 1947: 18; A. G. SMITH & GORDON, 1948: 208
- Ischnochiton clathratus* Reeve, 1847, var. *sinudentatus* Pilsbry, 1893 [= 1892], LELOUP, 1940: 3, 17 - 18
- Lepidozona sinudentata*, BURGHARDT & BURGHARDT, 1969: 22 - 23, 43 - 44; plt. 2, figs. 29 - 32 (in color) (with syn. *L. gallina* Berry, 1925); ABBOTT, 1974: 395 (with syn. *L. berryi* (Dall, 1919)); A. G. SMITH in LIGHT's Manual, 3rd ed., 1975: 463, 465
- Ischnochiton (decipiens* var. ?) *sinudentatus*, PILSBRY, 1898: 288
- Ischnochiton listrum* DALL, 1919: 504; OLDROYD, 1927: 271 - 272; BURGHARDT & BURGHARDT, 1969: 17; ABBOTT, 1974: 395; A. G. SMITH, 1977: 216, 227 (syn. of *L. sinudentata*)
- Ischnochiton (Ischnochiton) listrum*, DALL, 1921: 190
- Ischnochiton (Lepidozona) listrum*, A. G. SMITH, 1947: 18
- Ischnochiton berryi* Bartsch MS in BERRY, 1907: 51, *nomen nudum*
- Ischnochiton berryi* DALL, 1919: 507; 1921: 192; OLDROYD, 1927: 279; BURCH, 1942: 7; LIGHT's Manual, 2nd ed., 1954: 218; ABBOTT, 1974: 395 (? syn. of *Lepidozona sinudentata* (Carpenter in Pilsbry, 1892)); A. G. SMITH, 1977: 216, 220 (syn. of *L. sinudentata*)
- Ischnochiton (Lepidozona) berryi*, A. G. SMITH, 1947: 18; A. G. SMITH & GORDON, 1948: 207
- Lepidozona berryi*, BURGHARDT & BURGHARDT, 1969: 20, 44; plt. 2, fig. 32 (in color)
- Ischnochiton (Lepidozona) gallina* BERRY, 1925: 228 - 229; plt. 11, figs. 1, 2; A. G. SMITH, 1947: 18; A. G. SMITH & GORDON, 1948: 207, 208 [in error as *I. (L.) golischi* Berry, 1919]; A. G. SMITH, 1977: 216, 225 - 226 (syn. of *L. sinudentata*)

Ischnochiton gallina, WILLETT, 1935: 43-44 (syn. of *I. decipiens* Carpenter, 1892); ABBOTT, 1974: 395; fig. 4643 (syn. of *L. decipiens* (Carpenter in Pilsbry, 1892))

Nomenclatural Comments: By virtue of its high degree of intra-species variation, and its relatively wide bathymetric range, *Lepidozona sinudentata* has given rise to much confusion, and caused the description of several nominal species which have been found wanting in objective distinctions. The synonymization of *Lepidozona gallina* (Berry, 1925) imposed itself from the original description and accompanying photographs; it had been suggested already by WILLETT (1935) who considered *L. gallina* and *L. decipiens* conspecific, and by BURGHARDT & BURGHARDT (1969).

Lepidozona berryi (Dall, 1919), and *L. listrum* (Dall, 1919) were conclusively resolved as synonyms of *L. sinudentata* from direct examination of their respective holotypes kindly loaned by Dr. Joseph Rosewater, United States Museum of Natural History, Washington, D.C.

The case of *Ischnochiton decipiens* Carpenter in Pilsbry, 1892, was more complex. On subjective grounds, the species has been equated with *Lepidozona sinudentata*. The examination of a series of 6 small chitons in the collection of the Philadelphia Academy of Sciences (ANSP 42122) with the label "*I. decipiens sinudentatus* Cpr./Pacific Grove, nr. Monterey, Cal./H. Heath, Aug. 1," did not reveal any differences from other specimens of the very common (in the area) *L. sinudentata*; Pilsbry, in fact, had already referred Heath's specimens to *L. sinudentata* by citing them as "*Ischnochiton* (*decipiens* var.?) *sinudentatus* Cpr." (PILSBRY, 1898: 288). WILLETT (1935: 43-44) regarded *Ischnochiton decipiens* as a senior synonym of *I. (Lepidozona) gallina* Berry, 1925; and so did ABBOTT (1974: 395). BURGHARDT & BURGHARDT (1969: 21) cited *Lepidozona decipiens* with the added comment that "this species will probably turn out to be a synonym of *Lepidozona sinudentata*..." Recently, A. G. SMITH (1977: 223-224) concluded for the conspecificity of *Ischnochiton decipiens* and *I. berryi* Dall, 1919. Yet, on objective grounds, there is no way of knowing what the name *Ischnochiton decipiens* stood for. No type material was ever found (PALMER, 1958: 274), the species was never illustrated, and Carpenter's description as given by PILSBRY (1892: 123) is rather laconic and uninformative. Under the circumstances, it appears that *I. decipiens* should be considered a *nomen dubium* in as much as it can not be applied with certainty to any known taxon (ICZN, p. 151).

Type Material: The syntype series (Redpath Museum no. 27), available through the kindness of Dr. Vincent Condé, Redpath Museum, Montreal, Canada, carried the label [in white ink: ? Carpenter's own handwriting],

"*Ischnochiton sinudentatus* Cpr. (Type), California."

The series consists of 4 specimens. The largest of these specimens, measuring 12.0 mm in length, is here designated as **lectotype**; it is partly disarticulated, with loose valves i, vii, and viii, permitting verification of the slit formula indicated by PILSBRY (1892: 128) as 10-1-9. The other 3 specimens in the series are here designated as **paralectotypes**; they measure 10.0 mm, 6.7 mm, and 4.9 mm in length. The types are figured in PALMER (1958), the here designated lectotype in plt. 33, figs. 1-5, and the largest of the paralectotypes in plt. 30, figs. 8, 9. Color slides of the syntype series, as well as of the designated lectotype are deposited at CASIZ, Color Slide Series Nos. 2075-77 (A. G. Smith), and 3078-80 (AJF).

Ischnochiton berryi Dall, 1919: Holotype (USNM 193375), labelled "*Ischnochiton berryi*, Bartsch / (Fig'd type) / Pacific Grove." Color slides at CASIZ, Nos. 2960-61 (A. G. Smith) and 3094-95 (AJF).

Ischnochiton listrum Dall, 1919: Holotype (USNM 58,734). The label reads, "Type/ San Diego, Cal./ H. Hemphill." Color slides at CASIZ, Nos. 2562 (A. G. Smith), and 3117-18 (AJF).

Ischnochiton (Lepidozona) gallina Berry, 1925: Holotype, "A shell preserved dry S.S.B.757 entered as Cat. No. 4898 of the author's collection (ex-No. 1179, collection of R. H. Tremper)." Figured in BERRY (1925).

Type Locality: "California" as designated by Carpenter on the label attached to the type material. Following the suggestion implied in PILSBRY (1892: 128), the locality is here restricted to Monterey Bay (36°45'N, 121°55'W), Monterey County, California.

Diagnosis: chitons of small size (up to 2 cm), high-arched. Color very variable with rose, brown, and white predominating, often variegated. End valves and lateral areas of intermediate valves with radial ribs, variably granose. Central areas longitudinally ribbed, and latticed. Girdle scales, oval, only modestly convex, with shallow striae.

Description: **Lectotype**—Partly disarticulated. Length of the whole specimen (estimated) 12 mm [PALMER (1958: plt. 33, figs. 1-5) gives the length of the specimen as 14 mm]. The color of the tegmentum is a uniform light brown. Anterior valve and post-mucro area of posterior valve have distinctly granose radial ribs, well separated from each other. There are about 25 such radial ribs in valve i, and 18 in valve viii [the number of ribs is obscured by glue adhering to the valves]. In the intermediate valves, the lateral areas are distinct and bear 4-5 similar granose radial ribs. The ribs' granules are modest in size, almost obsolete at some points; they are larger, however, in the

posterior ribs, protruding discretely into the sutural spaces. Central areas have about 16 - 18 longitudinal riblets per sides, riblets that become crowded and obsolete towards the jugum to which they remain parallel. Valve ii shows a wedge figure composed of forwardly diverging jugal riblets. Cross-ribbing produces a latticing effect well marked on the pleural areas but less so at the jugum. Mucro is median, not prominent.

The articulamentum is white. Sutural laminae are semi-oval to quadrangular, relatively short. Sinus is relatively shallow; the sinus laminae show occasional irregular pectinations, and are separated from the adjacent sutural laminae by a minute notch. Teeth well cut, slightly beveled. Eaves solid. Slit formula 10-1-9. Girdle scales imbricated, oval, with about 10 shallow striae; maximum length about 200 μ m.

Another specimen (CASG 53074, coll. off Carmel, California, 9 July, 1935, at 6 fathoms, ex Hopkins Marine Station Collection), 12.0 mm in length, was used for SEM micrographs of the girdle scales (Figures 19, 29), and examination of the radula.

The radula measures about 7.0 mm in length, and has some 37 rows of teeth. Its relative length is 58%. The median plate is very wide anteriorly (140 μ m) where a thin blade recurves ventrally; the plate narrows medially (to 60 μ m), but bulges again posteriorly into a spheroid. The intermediate plate has a small knobby outgrowth in the outer-anterior corner. The uncinated plate is unicuspid; the blade measures about 200 μ m in length, the shaft about 350 μ m in length. A thick, blunt tubercle is seen on the upper part of the shaft, pointing inwardly.

The illustrated specimen, a topotype, (Figure 15, 16) of *Lepidozона sinudentata*, measures 15 mm in length, and was collected at the Breakwater, Monterey Bay, California, in 13 m of water, leg. A. J. Ferreira, September 1, 1973 (AJF 89).

Individual Variation: The considerable intraspecific variation in color and in sculpture displayed by *Lepidozона sinudentata* has left many collectors uncertain as to an understanding of the species, and bewildered by an array of names. In color, *L. sinudentata* varies from total white to dark brown, often variegated with reds, greens, oranges, sometimes even blue. Specimens of a varied color pattern may be found, and often are, side by side under

the same rock. A curious, and not uncommon color pattern, is that found on the type of *I. "gallina"* Berry, 1925, in which dark (red, maroon, or blue) transversal stripes alternate regularly with creamy-white colored ones for a zebra-like effect. It is interesting to note that there is some correlation between color pattern and depth, inasmuch as deep water specimens do not seem to vary as much in color patterns as shallow water ones do; with remarkable constancy, deep water specimens are a uniform medium brown, with no other color or pattern.

Variations in the sculpture of the radial ribs, particularly noticeable in the lateral areas have likely caused much uncertainty among collectors. As some of the illustrations here indicate (Figures 16, 17, 18), the radial ribs may vary considerably in their sculpture, boldness, number, and outline, from robustly built to absent, from coarse large granulations on the radial ribs to only minute nodules, from being well separated to being close together. In some specimens, only the granulations in the posterior rib are well marked, sometimes elongated, comma-like, protruding conspicuously into the sutural spaces; in some other specimens, the posterior rib may be non-granular, straight, or even absent. The correlation between these different forms and geography and depth is not clear cut: Northern specimens (Monterey) tend to have thicker and coarser radial ribs than southern specimens (San Diego); shallow specimens tend to have also bolder ribs in the lateral areas than deep water ones; a particular form of rib, with rather minute granules has only been found in deep water—and looked so different that for over two years, and until I examined more material from other deep water stations, I labored under the conviction of their being representatives of a new species. Variations in the central areas are not as frequent or obvious as those of the radial ribs in the lateral areas. Still, deep water specimens tend to have much more subdued longitudinal riblets, a greater number of them, more crowded together, resulting in a rather different appearance, particularly when combined with equally less marked cross-ribbing. Variation in other meristic characteristics is summarized in Table 1, based upon a random sample of 20 specimens from shallow water (down to 30 m), Monterey Bay, California.

Remarkably, the girdle scales were constant in their features in all specimens examined, despite differences in size, geography, or depth.

Explanation of Figures 28 to 33

Figure 28: *Lepidozона pectinulata*. Girdle scales. approx. $\times 100$

Figure 29: *Lepidozона sinudentata*. Girdle scales. approx. $\times 200$

Figure 30: *Lepidozона willetti*. Girdle scales. approx. $\times 1000$

Figure 31: *Lepidozона willetti*. Girdle scales. approx. $\times 600$

Figure 32: *Lepidozона guadalupensis* Ferreira, spec. nov. Girdle scales approximately $\times 300$

Figure 33: *Lepidozона guadalupensis* Ferreira, spec. nov. Girdle scales approximately $\times 100$

SEM micrographs by Hans Bertsch



Figure 28



Figure 29



Figure 30



Figure 32



Figure 31



Figure 33

In size, *Lepidozona sinudentata* only rarely attains 2 cm in length. The largest specimen examined measures 24.5 cm (including girdle) in length; its slit formula was 12-1-12 (CASIZ, Camalu, Baja California, Mexico, leg. L. D. Miles, Apr. 24, 1951, ex Miles Colln.).

Distribution: *Lepidozona sinudentata* seems to have a continuous distribution between latitudes 28° N and 38° N. The northernmost record is Salt Point Ranch (38° 39' N, 123° 19' W), Sonoma County, California (LACM 64-6, at 13 m, leg. J. H. McLean, February 21, 1964). The southernmost record is Thurloe Head (27° 37' 31" N, 114° 50' 37" W), outer coast of Baja California, Mexico (LACM 71-170, 13-20 m, leg. J. H. McLean & P. LaFollette, *R/V Searcher*, October 23, 1971). There were many stations in between including collections at the offshore islands of San Geronimo (LACM 67-62), Sacramento Reef (LACM 71-91), San Martin (CASG 27600; LACM 67-60), Coronados (LACM 63-41; UCLA 22372 & 22383), San Nicolas (LACM 69-15), Catalina (UCLA 22319, 22381 & 22386; LACM 65-6; LACM-AHF 1359-41, 1381-41, 1399-46, 1426-41 & 1624-48; CASG 41308), Santa Rosa (LACM 73-9), Santa Cruz (LACM 63-5 & 73-11; LACM-AHF 1286-41), San Miguel (LACM 67-38) and Farallon (LACM 62-9).

Bathymetrically, *Lepidozona sinudentata* has been found from intertidal to about 200 m (LACM-AHF 1359-41, "100-108 fathoms, on gray sand, 1¾ miles east of White Cove, Santa Catalina Island, Los Angeles, California . . . June 13, 1941," 1 specimen).

Remarks: The marked variability in *Lepidozona sinudentata* deserves emphasis. Interesting is the color phase "gallina" with its zebra-like appearance. Color variation in chitons is found in many species, but this particular zebra pattern is uncommon. However, it may be seen in two other species not immediately related: *Ischnochiton petaloides* (Gould, 1846) [= *I. mariposa* Dall, 1919] from the eastern Pacific and *Ischnochiton zebrinus* Bergenhayn, 1933 from the Sea of Japan.

But the variations in sculpture, particularly of the lateral areas, should be stressed inasmuch as they may cause, and likely have caused, the false impression of distinct species. The deep water specimens may be particularly troublesome. It was only when, thanks to the kindness of Dr. James H. McLean, I had the opportunity of examining material in the Allan Hancock Foundation Collection, now with the Los Angeles Museum of Natural History, from several deep-water stations in the general area of Catalina Island, Los Angeles County, California (LACM-AHF 1259-41, 1286-41, 1359-41, 1381-41, 1383-41, 1426-41, 1399-46, 1624-48), that I realized the full

scope of intraspecific variation in *L. sinudentata*, and was led to adopt an even broader view of the species than, under the auspices of A. G. Smith, I had anticipated.

Lepidozona scabricostata (Carpenter, 1864)

(Figures 7, 8, 24, 25)

- Ischnochiton* (*Lepidopleurus*) *scabricostatus* CARPENTER, 1864b: 612 (Reprinted, 1872: 98), *nomen nudum*; A. G. SMITH, 1977: 216, 234-235
- Lepidopleurus scabricostatus* CARPENTER 1864b: 649 (Reprinted, 1872: 135); 1866: 212; COOPER, 1867: 22; LOWE, 1904: 19 [in error as "*crebriostatus*"]
- Ischnochiton* (*Ischnochiton*) *scabricostatus*, PILSBRY, 1892, 14: 121; 1893, 15: 76, pl. 16, figs. 55, 56; DALL, 1921: 191; A. G. SMITH, 1947: 18
- Ischnochiton scabricostatus*, PILSBRY, 1896: 49-50; 1898: 288; KEEF, 1904: 349; OLDROYD, 1927: 276; PALMER, 1945: 101 [as "*I. subexpressus* Cpr. type = *scabricostatus* Cooper No. 518a . . ."]; 1958: 296; pl. 30, figs. 10-12; BURGHARDT & BURGHARDT, 1969: 18; ABBOTT, 1974: 395
- Ischnochiton* (*Lepidozona*) *golischi* BERRY, 1919, 2 (6): 7; 1925, 16 (5): 229-231; pl. 11, figs. 3, 4; A. G. SMITH, 1947: 18; A. G. SMITH & GORDON, 1948: 207-208 [in error for *I. (L.) gallina* Berry, 1925]; A. G. SMITH, 1977: 216, 226 (syn. of *L. scabricostata*)
- Ischnochiton* (*Ischnochiton*) *golischi*, DALL, 1921: 192 (in section *Lepidozona*)
- Ischnochiton golischi*, OLDROYD, 1927: 284 (in section *Lepidozona*); TALMADGE, 1973: 232
- Lepidozona golischi*, BURGHARDT & BURGHARDT, 1969: 21-22; ABBOTT, 1974: 396, fig. 4647
- Lepidozona inefficax* BERRY, 1963: 138; ABBOTT, 1974: 396

Nomenclatural Comments: CARPENTER's (1864b) original description of *Ischnochiton scabricostatus* was both inadequate and confusing. PILSBRY's (1893, 15: 76; pl. 16, figs. 55, 56) redescribed and figured the species based upon the only specimen known at the time (USNM 16268). Still, the difficulties remained, and in collections specimens were often found labelled as *Ischnochiton* (*Lepidozona*) *golischi* Berry, 1919. Examination of the holotype of *Ischnochiton scabricostatus* Carpenter, 1864, made available through the courtesy of Dr. Joseph Rosewater, United States National Museum, Washington, D.C., solved conclusively the identification problem. A specimen (ANSP 72128) subsequently reported and labelled as *Ischnochiton scabricostatus* by PILSBRY (1898: 288) loaned for study through the kindness of Dr. Robert Robertson, Academy of Natural Sciences, Philadelphia, confirmed the correctness of its synonymy with the later-named *I. golischi*. The examination of the holotype of *Ischnochiton* (*Lepidozona*) *golischi* Berry, 1919, and the only extant paratype of *Lepidozona inefficax* Berry, 1963, made available through the generous hospitality and cour-

tesy of Dr. S. Stillman Berry, Redlands, California, September 21, 1974, revealed their conspecificity with *Lepidozona scabricostata*.

Diagnosis: Chitons of small size (up to about 2 cm), high arched. Color uniform, orange-brown to creamy-white. End valves and lateral areas display flattish radial ribs, neatly separated by sulci, and bearing a row of small round tubercles (often eroded away). Central areas with longitudinal riblets with a tendency to become beaded, and only faintly latticed. Girdle scales imbricated, moderately convex, shallowly striated.

Type Material: Holotype (USNM 16268), figured in PILSBRY (1893, 15: plt. 16, figs. 55, 56) and PALMER (1958: plt. 30, figs. 10-21); color slides at CASIZ, Nos. 2974-77 (A. G. Smith), and 3119 (AJF). Other type material deposited by Carpenter in the "State Collection, no. 1071 c" [which refers to the old California State Collection] is presumed lost.

Ischnochiton (Lepidozona) golischi Berry, 1919: "Type—An animal preserved dry [S.S.B. 1068], entered as Cat. No. 4093 of the author's collection. A paratype [S.S.B. 1067] is the property of the Southwest Museum, Los Angeles." (BERRY, 1925: 230).

Lepidozona inefficax Berry, 1963: Holotype, "No. 28,712 Berry Collection", has been lost (Dr. S. S. Berry, personal communication, Sept. 21, 1974). One paratype, still attached to the shell of the brachiopod *Terebratalia*, in the Berry Collection; color slides of the paratype at CASIZ, Nos. 3115-16 (AJF).

Type Locality: "Catalina Island [California] 10-20 fms . . ." [18-36 m] (CARPENTER, 1866: 212).

Description: The specimen [not figured here] is oval, high arched, carinated, uniformly brown in color. Fully extended, preserved in ethyl alcohol, it measures 21.5 mm in length (including girdle), 12.0 mm in width, and 3.5 mm in height. Width/length ratio: 0.55. Jugal angle about 93°.

The anterior valve displays about 40 flat radial ribs separated from each other by a shallow sulcus, and bearing a row of small (about 100 μ m in diameter) round tubercles. Most of these tubercles are missing, obviously eroded away; but it may be estimated that there would be about 12 per rib. The posterior valve shows about 30 of such tuberculated ribs in the post mucro area. The lateral areas of the intermediate valves are well defined; they bear 6-7 similar flat, tuberculated ribs, many of the tubercles missing. Central areas have about 24 longitudinal riblets per side, with rather faint cross-ribbing; the longitudinal riblets tend to become obsolete towards the jugum, and often

are definitely granular, quasi-beaded. The jugal tract diverges forwardly on valve ii, outlining a wedge-like figure. Mucro is moderately anterior.

The gills, about 30 on each side, extend from about 1 mm in front of the anus to 2 mm behind the anterior border of the foot. The girdle, about 1.5 mm in width, is covered by imbricating, oval, flattish, scales, measuring as much as 220 μ m in length, and displaying some 10-12 shallow striations.

The specimen, a topotype, was collected off Empire Landing, Catalina Island (33°26' N, 118°29' W), California, in 79 m of water [43 fathoms] (CASIZ, leg. D. P. Abbott, Feb. 9, 1949, ex R. Stohler). Color slides at CASIZ, No. 590.

A second specimen collected at 365-730 m [200-400 fathoms] off Cordell Bank (38°03' N, 123°32' W), California (CASG 43983, *USS Mulberry*, station 56, March 29, 1950) is illustrated here (Figures 7, 8).

A third specimen collected at 365 m [200 fathoms] off False Cape (40°31' N, 124°24' W), Humboldt County, California, (CASIZ, *M/V Flicker*, Sept. 1967, ex R. R. Talmadge) measures 22.9 mm in length, and was used for the study of the articulamentum, radula, and SEM micrographs of the girdle scales (Figures 24, 25).

The articulamentum of this specimen is white. Sutural laminae are sharp and semioval, separated by a relatively shallow sinus. The sinus laminae are irregularly pectinated, and demarcated from the adjacent sutural laminae by a minute notch. Eaves are solid. The teeth are sharp edged and straight. Slit formula 12-1-11.

The radula measures 8.4 mm in length, and has 38 rows of teeth. Radula relative length 37%. The median plate is enlarged anteriorly (130 μ m), where it bears a thin blade recurved ventrally; it narrows medially but only moderately (to about 50 μ m); posteriorly it bulges again (to about 80 μ m) in a spheroid. The intermediate plates have a knobby outgrowth at the outer-anterior corner. The uncinated plate is unicuspid; the blade measures about 180 μ m in length, the shaft 600 μ m. No tubercle is seen in the upper part of the shaft or the uncinated plate, nor in the radula of another specimen examined from the same station.

Individual Variation: All specimens tend to be uniformly colored. Some were an intense orange "Caledonian" brown, others a much lighter color, almost white. Variations in meristic characteristics are summarized in Table 1. The largest specimen examined measures, including the girdle, 24 mm in length (CASIZ, off Point Joe, Monterey Peninsula, Monterey County, California, in 110-130 m of water [60-70 fathoms], leg. C. Jones, May 1941, ex Wilfred Mack Colln.).

Table 1

	<i>Lepidozona mertensii</i> (n=20)	<i>Lepidozona cooperi</i> (n=20)	<i>Lepidozona pectinulata</i> (n=20)	<i>Lepidozona sinudentata</i> (n=20)	<i>Lepidozona scabricostata</i> (n=12)	<i>Lepidozona willetti</i> (n=10)	<i>Lepidozona retiporosa</i> (n=20)	<i>Lepidozona guadalupensis</i> (n=12)
length (mm)	30-42	18-42	17-39	13-22	10-24	10-20	8-17	12-25
width (mm)	16-21	10-22	9-20	8-12	7-13	4-10	5-11	9-15
width/length ratio (mean)	0.59	0.57	0.58	0.56	0.58	0.61	0.61	0.63
jugal angle (mean)	93°	92°	99°	92°	98°	99°	99°	104°
Tegmentum:								
Valve i-ribs (no.)	21-40	15-24	16-35	18-29	32-50	20-40	20-30	12-26
(mean)	27.7	21.0	24.5	22.5	40.0	29.8	25.5	18.3
Valves ii-vii								
central areas								
riblets (no.)	10-14	10-22	13-20	13-19	19-22	16-22	30-40+	11-16
latticed?	yes	yes	yes	yes	yes	yes	yes "pitted"	yes
"wedge" on ii?	yes	yes	yes	yes	yes	yes	no	yes
lateral areas								
ribs (no.)	5-8	3-8	4-6	3-5	4-7	4-7	3-6	3-6
(mode)	6	5	4	4	5	5	5	4
(sculpture?)	tubercles round (200 µm)	tubercles elongated	granular	granose (variably)	tubercles round (100 µm)	tubercles round (100 µm)	tubercles round (80 µm)	tubercles round (200 µm)
Valves viii-ribs (no.)	11-23	15-20	12-30	12-27	25-40	15-28	15-20	13-20
(mean)	17.5	16.7	20.3	16.8	30.0	21.0	17 ?	15 ?
mucro?	ant./cent.	cent.	cent.	cent.	ant.	ant.	ant.	ant./cent.
Articulamentum:								
Valve i-slits (no.)	8-12	9-15	10-15	7-11	10-13	10-11	8-13	9-11
(mode)	10	10	12	9	12	10	11	11
Valve viii-slits (no.)	8-11	9-14	10-17	7-11	11-14	9-11	8-12	9-11
(mode)	10	10	15	9	11	10	10	11
Girdle scales:								
flat-striated (S) or convex mammillated (M)?	M	S	M	S	S	M	S	M
maximum length (µm)	500	500	400	300	250	400	200	500

In some specimens the longitudinal riblets of the central areas are definitely granose to beaded. Some specimens display also what could be called growth lines in the form of transversal rugae particularly noticeable on valve ii.

Distribution: *Lepidozona scabricostata* appears to have a continuous distribution between the latitudes 28° N and 48° N. The northernmost record is Cape Flattery (48° 24.7' N, 126° 06.2' W), Washington (LACM 72-140, FRB sta. 72-Q-3, at 274 m, leg. D. Quayle, Feb. 1972). The southernmost record is that given by BERRY (1963) for *L. "inefficax"*, Sebastian Vizcaino Bay (28° 26.5' N, 114° 36' W) Baja California, Mexico, at 55-57 fathoms [99-103 m]. There are many stations between these extremes. Although it has been found intertidally (LACM 63-53, Ensenada, Baja California, leg. J. H. McLean, Nov. 29, 1963, 12 specimens), *L. scabricostata* is confined to relatively deep water. Records from the offshore island

are as follows: San Clemente (LACM-AHF 911-39, at 60-85 fathoms [108-153 m]), San Nicolas (LACM-AHF 1345-41, at 57 fathoms [103 m]), Catalina (LACM-AHF 3310-55, at 47-52 fathoms [85-94 m]); UCLA 22403, at 40 fathoms [72 m]), Santa Rosa (LACM-AHF 1385-41, at 75-76 fathoms [135-137 m]). Santa Cruz (LACM-AHF 1196-40, at 110-140 fathoms [198-252 m]), and Anacapa (LACM-AHF 874-38, 45 fathoms [81 m]). The greatest depth at which the species has been found is 1 260-1 460 m [690-800 fathoms] (CASG 43981, Mulberry Seamount, USS Mulberry station 38, February 13, 1950).

Remarks: There is a great similarity between *Lepidozona scabricostata* and *L. willetti* (Berry, 1917). The two species seem to agree in almost every respect except their radically different girdle scales. To make the matter all the more interesting, the two species are sympatric, often being found together in the same station, and exhibiting

exactly the same golden brown color. Both *L. scabricos-tata* and *L. willetti* differ from *L. mertensii* in several respects, above all by their girdle scales, the presence of sulci between the radial ribs, and the size of the tubercles on those ribs. From the examination of specimens of comparable size, it was learned that the tubercles of *L. scabricos-tata*, as well as those of *L. willetti*, measure about 100 μm in diameter whereas those of *L. mertensii* averaged 200 μm in diameter.

Lepidozonia willetti (Berry, 1917)

(Figures 9, 10, 30, 31)

- Ischnochiton (Lepidozonia) willetti* BERRY, 1917: 232, 236-238, figs. 1, 2; A. G. SMITH, 1977: 216, 238
Ischnochiton willetti, WILLETT, 1919: 27; OLDROYD, 1924: 192-193; LAROCQUE, 1953: 13 (in section *Lepidozonia*)
Ischnochiton (Ischnochiton) willetti, DALL, 1921: 192 (in section *Lepidozonia*)
Lepidozonia willetti, BURGHARDT & BURGHARDT, 1969: 23; ABBOTT, 1974: 395
Ischnochiton (Lepidozonia) catalinae WILLETT, 1941: 185-186; plt. 31, fig. 2; A. G. SMITH, 1947: 18; A. G. SMITH & GORDON, 1948: 207 [error in identification, A. G. SMITH, 1977: 222]; A. G. SMITH, 1977: 216, 222 (syn. of *L. willetti*)
Lepidozonia catalinae, BURGHARDT & BURGHARDT, 1969: 20-21; ABBOTT, 1974: 396

Nomenclatural Comments: The conspecificity of *Lepidozonia willetti* and *L. catalinae* was established through the examination and side by side comparison of type materials of both nominal species, namely, *L. willetti*, paratype (UCLA 22314) available through the courtesy of Dr. W. P. Popenoe and Mrs. LouElla Saul, University of California, Los Angeles; *L. willetti* virtual paratype (CASG 43991) through the cooperation of Dr. Peter U. Rodda, California Academy of Sciences, Department of Geology, San Francisco; and *L. catalinae* holotype (LACM 1063), through the kindness of Dr. James H. McLean, Los Angeles County Museum of Natural History, Los Angeles, California.

Diagnosis: Chitons of medium size (up to 3 cm), oval, high arched. Uniformly colored reddish-brown. End valves and lateral areas show flattish radial ribs separated by sulci, and bearing small round tubercles. Central areas with longitudinal riblets, often faintly beaded, and weakly latticed. Mucro is anterior. Girdle with imbricated, strongly convex scales bearing a rather long, striated, mammilla.

Type Material: Holotype - "A shell preserved dry [S.S.B 159] as Cat. No. 3700 in the author's collection". (BERRY, 1917: 238). Paratypes - "... in the collections of the California Academy of Sciences [CASG 1123], the Academy of Natural Sciences of Philadelphia [ANSP 117530], the United States National Museum [USNM 217936], and the private collection of Mr. George Willett [UCLA 22314]" (BERRY, l.c.).

Ischnochiton (Lepidozonia) catalinae Willett, 1941: Holotype (LACM 1063). Paratypes (UCLA 22320 ex G. Willett Colln.; LACM 1000; CASG 10263 ex A. G. Smith Colln.; ANSP 117536).

Type Locality: "15-20 fathoms [27-36 m], Forrester Island, Alaska; George Willett, May-July-August, 1914-1916; 36 specimens." (BERRY, l.c.)

Description: BERRY's (1917) original description and figuring is perfectly adequate to define and understand the species.

The photographed specimen (Figures 9, 10) is a paratype (CASG 1123). Color slide at CASIZ, No. 3101 (AJF). It shows that the longitudinal riblets in the central area remain parallel to the jugum or even display a mild tendency to converge forwardly. However, the jugal tract supersedes them on valve ii where it diverges forward widely forming a wedge-like figure. The tubercles of the radial ribs measure about 100-150 μm in diameter and height. The girdle scales, strongly convex and with long nipples measure a maximum of 270 μm in length. Mucro is anterior.

Another specimen (SDNH 23505), a topotype, was used for color slides of the girdle scales, now at CASIZ, Nos. 3126-27 (AJF).

A third specimen was used to obtain SEM micrographs of the girdle scales (Figures 30, 31), and study of the radula. The specimen, dried but fully extended measures 16.5 mm in length (CASG 32536, San Pedro, California, San Diego Marine Biology Association sta. no. XXI-2, at 79-140 m, June 20, 1901). Slit formula 10-1-10.

The radula of this specimen measures 6.3 mm in length, and has 38 rows of teeth. Relative length 38%. The median plate is wide anteriorly (140 μm) with a thin blade that recurves ventrally; the plate narrows medially (to 50 μm) and then bulges posteriorly (to 80 μm) to terminate abruptly in a point. The intermediate plate shows a knobby outgrowth on the outer-anterior corner. The uncinated plate is unicuspid; the blade is about 250 μm in length, the shaft 500 μm . A tubercle is discernible on the

upper part of the shaft, immediately below the blade, pointing inwardly.

Individual Variation: Variations in meristic characteristics are summarized in Table 1. It is noteworthy that all specimens examined were of a very constant reddish-brown color, uniform throughout, and practically with no markings. Only two specimens showed a small dark brown triangular marking at the jugum; and one specimen was a light tan color, vaguely splashed with cream-white. The largest specimen examined measures 28.0 mm in length (including girdle); the largest specimen reported is 29.5 mm long (BERRY, 1917).

Distribution: *Lepidozona willetti* seems to have a continuous distribution between latitudes 26° N and 54° N. The northernmost record is Forrester Island (54° 48' N, 133° 32' W), Alaska (Type locality); the southernmost record is 29 miles [46.4 km] south of Punta Abreojos (26° 16' 24" N, 113° 41' 18" W) Baja California, Mexico (LACM-AHF 1710-49, at 54 fathoms [99 m], March 7, 1949). The species was collected at many stations between these two extreme points, including Catalina Island (LACM 65-7, 1000, 1063; SDNH 41430; UCLA 22320), Anacapa Island (LACM-AHF 875-38), and Forrester Island (CASG 43991; SDNH 23505; UCLA 22314). It definitely favors relatively deep water with no record of having been found intertidally; the bathymetric range of the examined specimens that had it noted is 13 - 40 m [40 - 125 feet] (LACM 60-24, Carmel Submarine Canyon, north end of San Jose Creek, Monterey County, Calif., leg. J. H. McLean, 1960 - 1964) to 274 m, west of Cape Flattery (48° 24' N, 126° 06' W) Washington (LACM-AHF 72-140, leg. D. Quayle, FRB sta. t2-Q-3, Feb. 1972).

Remarks: *Lepidozona willetti* has been found together with *L. mertensii* (BERRY, 1917); however, as mentioned before it is most often found together with *L. scabricostata* with which it shares a great portion (if not all) of its bathymetric and geographic range. A color slide of the two species, side by side, is in CASIZ, No. 3113 (AJF), emphasizing their great morphological and color similarity.

Lepidozona retiporosa (Carpenter, 1864)

(Figures 11, 12, 26, 27)

Ischnochiton (*Trachydermon*) *retiporosus* CARPENTER, 1864b: 603 (Reprinted, 1872: 89), *nomen nudum*; *ibid.*, 649 (Reprinted, 1872: 135); 1865: 59 - 60; PILSBRY, 1892, 14: 75; A. G. SMITH, 1977: 216, 233
Trachydermon retiporosus, COOPER, 1867: 22

Ischnochiton retiporosus, PILSBRY, 1893: 77; plt. 16, figs. 47, 50 - 53 [in error as "*reteporosus*"]; KEEP, 1904: 349 [as "*reteporosus*"]; WILLETT, 1919: 27; OLDROYD, 1924: 190 - 191; 1927: 272 - 273 (in section *Stenoradsia*); BURCH, 1942: 7; LAROCQUE, 1953: 13 (in section *Stenoradsia*); BURGHARDT & BURGHARDT, 1969: 17 - 18, 43; plt. 2, fig. 21 (in color); KUES, 1974: 366; ABBOTT, 1974: 395
Ischnochiton (*Ischnochiton*) *retiporosus*, DALL, 1921: 191
Ischnochiton (*Lepidozona*) *retiporosus*, BERRY, 1917: 231, 235 - 236; 1927: 164; A. G. SMITH, 1947: 18; A. G. SMITH & GORDON, 1948: 208; PALMER, 1958: 275; plt. 30, fig. 7; plt. 35, figs. 4, 5
Lepidozona retiporosa, CARLISLE, 1969: 241
Leptochiton punctatus WHITEAVES, 1887
Ischnochiton venezius DALL, 1919: 509; BURGHARDT & BURGHARDT, 1969: 18; ABBOTT, 1974: 395; A. G. SMITH, 1977: 216, 237 - 238 (syn. of *L. retiporosa*)
Ischnochiton (*Ischnochiton*) *venezius*, DALL, 1921: 191; OLDROYD, 1927: 274; A. G. SMITH, 1947: 18
Ischnochiton (*Ischnochiton*) *aureotinctus* Carpenter MS, PILSBRY, 1892, 14: 123; DALL, 1921: 191; A. G. SMITH, 1977: 216, 220 (as *nomen inquirendum*)
Ischnochiton aureotinctus, KEEP, 1904: 349; OLDROYD, 1927: 276 - 277; PALMER, 1945: 101; BURGHARDT & BURGHARDT, 1969: 16
Ischnochiton (*Lepidozona*) *aureotinctus*, A. G. SMITH, 1947: 18; PALMER, 1958: 272, plt. 31, figs. 1 - 4

Nomenclatural Comments: The examination of the holotype of *Ischnochiton venezius* Dall, 1919, available through the courtesy of Dr. Joseph Rosewater, United States Museum of Natural History, Washington, D.C., revealed its conspecificity with *Lepidozona retiporosa* as suspected by BURGHARDT & BURGHARDT (1969) and confirmed by A. G. SMITH (1977).

The synonymization of *Ischnochiton* (*Ischnochiton*) *aureotinctus* Carpenter in Pilsbry, 1892 was not an easy matter. Examination of the the holotype, kindly loaned by Dr. Vincent Condé, Redpath Museum, Montreal, Canada, first led to the conclusion that this nominal species should remain as a *nomen inquirendum* pending the availability of more and better material. A. G. SMITH (1977). The *desideratum* has now been fulfilled in the form of several lots from deep water in the Allan Hancock Foundation Collection, now at the Los Angeles County Museum of Natural History, available through the generous cooperation of Dr. James H. McLean. The material contained several specimens that revealed the intergradation of *I. aureotinctus* with *L. retiporosa*, and establishes their conspecificity.

Diagnosis: Chiton small (up to 1.5 cm), color uniform, often ashen-brown. End valves and lateral areas show ill-defined radial ribs bearing a row of minute tubercles (often eroded away). Central areas punctated to pitted.

Mucro anterior. Girdle scales closely imbricated, small, elongated, striated.

Type Material: Holotype (USNM 4499). Color slide of the specimen at CASIZ, No. 2045 (A. G. Smith).

Ischnochiton venezius Dall, 1919: Holotype (USNM 216792). Color slides at CASIZ, Nos. 2966-67 (A. G. Smith), and 3123-24 (AJF).

Ischnochiton (Ischnochiton) aureotinctus Carpenter in Pilsbry, 1892: Holotype (Redpath Museum no. 26). Color slide of the specimen, CASIZ, No. 3088 (A. G. Smith).

Type Locality: Puget Sound, Washington, "specimen unicum legit Kennerley" (Carpenter, 1865: 59).

Description: The specimen (Figures 11, 12) is oval, high arched, of a dusty brown color. Dried but fully extended, it measures 13.0 mm in length, 8.2 mm in width, and 2.8 mm in height. Width/length ratio: 0.63. Jugal angle about 98°.

The anterior valve shows some 30 radial ribs, quasi-obsolete, almost undefined except for the row of minute tubercles which they bear. These tubercles, most of which have fallen off, are neatly round, and measure about 80 μ m in diameter and height. Allowing for those that must have fallen off, it is estimated that there would be about 10 such tubercles per rib. Similar sculpture is found in the post-mucro area of the posterior valve; only here the ribs are even less defined, and a reasonable count could not be obtained. The mucro of the posterior valve is well marked, slightly beaked, and definitely anterior. The intermediate valves show fairly raised and demarcated lateral areas bearing similar tuberculated ribs, about 5-6 ribs per lateral area. It must be stated that the radial ribs are only virtual, *i.e.*, not defined by any feature, such as sulci or undulations of the tegmentum, other than the presence of the minute tubercles. The central areas are punctated to pitted, but become rather granulose at the jugum; in the pleural areas it becomes apparent that the pitted appearance is the result of the intercrossing of longitudinal and transversal riblets, an accentuated case of latticing. No wedge-like figure is found on valve ii.

The articulamentum is creamy white. Sutural laminae are rather short, and semioval. Sinus is shallow; sinus laminae with minute, irregular pectinations, occasionally notched at their junction with the sutural laminae. Eaves are solid. Insertion teeth are sharp and straight edged. Slit formula 12-1-11.

The girdle is densely covered with imbricating elongated scales, about 150 μ m in length by 70 μ m in width. The scales have 8-10 striations, which are minutely punctated, a feature particularly visible in SEM micrographs (Figures 26, 27). The specimen, a topotype, was collected

at 48 m Puget Sound, Washington (CASG 43840, *leg.* T. S. Oldroyd, *ex* Gordon Colln.).

A second specimen (CASG 36334, off San Pedro, Calif., San Diego Marine Biological Association sta. XXIII-2, June 22, 1901), collected in 42-55 m, was used for the study of the radula. The specimen measures 11.0 mm in length. The radula measures 4.2 mm, and has 37 rows of teeth. Radula relative length 38%. The median plate is wide anteriorly (80 μ m) bearing a thin blade that recurves ventrally; the plate narrows medially (to about 40 μ m), and bulges modestly (to about 50 μ m) posteriorly. The uncinated plate is unicuspid; the blade measures about 80 μ m in length, the shaft 140 μ m. In the upper part of the uncinated plate, immediately underneath the blade a tubercle, about 50 μ m \times 10 μ m points inwardly.

Individual Variation: In coloration, *Lepidozonia retiporosa* varies relatively little; it usually remains in tones of brown, occasionally being tan or apricot color. Girdle is usually the color of the tegmentum, and only occasionally banded. In sculpture, there is some observable variation in the number of tubercles present in the lateral areas and end valves. Some specimens may have very few tubercles, even none, making identification rather difficult and tentative. For whenever the tubercles are absent (which may be the result of erosion; or, in juvenile specimens, in which the tubercles might not yet have appeared?) the lateral areas look rather smooth since the radial "ribs" are virtual; in such instances the other characteristics of the species, notably its girdle scales, the pitted appearance of the central areas (not always clearly present, either, particularly in juvenile specimens), and the anterior mucro may help in identification.

Variations in meristic characteristics are summarized in Table 1, based upon a sample of 20 adult-looking specimens from several geographical sites.

In size, the largest specimen examined measures 17.0 mm in length, including girdle (CASG 43980).

Distribution: The known range of *Lepidozonia retiporosa* extends between latitudes 23° N and 55° N, from intertidal in the northern part of the range to considerable depths in the southern areas. The northernmost record is Edna Bay (55° 57' N, 133° 40' W), Kosciusko Id., Alaska, (CASIZ, *leg.* G. D. Hanna, intertidal, July 1947). Until recently the southernmost record had been placed around San Diego, California; but dredging along the outer coast of Baja California, Mexico has shown that, at considerable depths, *L. retiporosa* is to be found much farther south, and that its range extends south at least to the tip of Baja California (23° 45' N, 111° 55' W) (KUES, 1974).

The known bathymetric ranges extend from intertidal to 690-800 fathoms [1262-1463] (CASG 33036, Mul-

berry Seamount, *USS Mulberry* sta. 38, leg. G. D. Hanna, February 13, 1950).

Between the two extreme points of its range, the species has been collected at many stations, notably at Catalina Island (CASG 43988; LACM A.199 & HH.1052; LACM-AHF 999-39, 1399-41, 1426-41), Vancouver Island (CASG 37544; LACM 37-2, 73-40, 73-43), Hope Id. (LACM 63-62), Jessie Island (LACM A.8881.66).

Remarks: The characteristically "pitted" appearance of the central areas makes *L. retiporosa* quite unique among the *Lepidozona* in the eastern Pacific. The species is sympatric with *L. scabricostata* and *L. willetti* to the point that the 3 species are often seen together at the same collecting station. Interestingly, they often share exactly the same color.

Lepidozona guadalupensis Ferreira, spec. nov.

(Figures 13, 14, 32, 33)

"*Ischnochiton mertensi* (Middendorff)", CHACE, 1958: 331 [not *Lepidozona mertensii* (Middendorff, 1847)]

"*Lepidozona mertensi* (Middendorff, 1846)", A. G. SMITH, 1963 (4): 148 [not *Lepidozona mertensii* (Middendorff, 1847)]

Diagnosis: Medium size chitons (up to 3 cm). Color in tones of red, and orange-brown, often variegated. End valves and lateral areas with radial ribs separated by well defined sulci, and bearing a row of well-formed, round, tubercles. Central areas with longitudinal riblets, cross-ribbed. Girdle scales imbricated, strongly convex, nipped, and with very minute rows of granules on their outer faces.

Description: Holotype – Dried but fully extended, it measures (including the girdle) 22.0 mm in length, 14.0 mm in width, and 3.6 mm in height. Width/length ratio: 0.63. Jugal angle about 103°.

The tegmentum has a predominantly pink color mixed with light tan and brown; the surface is microgranular. The anterior valve shows some 14 radial ribs bearing 8 - 12 (some eroded away) round and well defined tubercles about 200 µm in diameter and height. Each radial rib is clearly separated from adjacent ones by sulci marked by a row of minute and somewhat irregular pits. The post-mucro area of the posterior valve has similar radial ribs, about 14 in number. The lateral areas of the intermediate valves are moderately raised, and show about 5 - 6 similar radial tuberculated ribs. The central areas display longitudinal riblets about 12 - 14 per side, cross-ribbed; the longitudinal riblets become progressively crowded towards the jugum. The jugum is also ribbed longitudi-

nally, and shows cross ribbing although not as clearly as in the pleural areas. The jugal tract tends to diverge forwardly, particularly on valve ii where it forms a wedge-like figure. This wedge figure shows cross-ribbing, too. In the posterior valve, the mucro is anterior, but not conspicuous.

The articulamentum is white. Sutural laminae are sub-quadrate and relatively short, separated by a well defined sinus. Sinus laminae show a few minute, irregular pectinations, and are demarcated from the adjacent sutural laminae by a small notch. The eaves are solid. The insertion teeth are relatively small, sharp, straight edged. Slit formula 9-1-11.

The girdle is distinctly banded pink and tan. The girdle scales are large (up to 500 µm), strongly convex, and often bearing a nipple. SEM micrographs of the girdle scales (Figures 32, 33) show this nipple to be striated; they show further that the outer surface of the scales bear transversal rows of minute pustules which, when seen under ordinary magnifications, may give an impression of striation.

The radula measures 8.0 mm in length, and has 35 rows of teeth. Its relative length is 36%. The median plate is wide anteriorly (170 µm) with a thin blade recurved ventrally; the plate narrows medially (to 50 µm) and then bulges posteriorly (to 80 µm) in a spheroid that seems to end in two points separated by a notch. The intermediate plate has a knobby outgrowth on the outer-anterior corner. The uncinated plate is unicuspid; the blade is about 250 µm, the shaft 500 µm. In the upper part of the shaft, underneath the blade, a tubercle is present, pointing inwardly.

The specimen here designated as holotype was collected at Northeast Anchorage (29°11'N; 118°17'W), Guadalupe Island, Baja California, Mexico, December 30, 1974, in about 0.5 m of water, at low tide, on the undersurface of a small movable rock, leg. W. L. Lee & A. J. Ferreira (AJF 210) as part of a lot of four specimens.

One of these specimens, a paratype, 25 mm in length is illustrated (Figures 13, 14).

Type Material: In addition to the holotype, and 3 paratypes from the same station, a lot of 15 other specimens, collected during the same trip to Guadalupe Island, at Sealers' Camp (29°01'N; 118°13'W), also at low tide, under rocks (AJF 211, leg. W. L. Lee & A. J. Ferreira, January 1 - 2, 1975) are also designated here as paratypes.

Holotype (disarticulated valves, mounted radula, and mounted girdle scales) is deposited in the California Academy of Sciences (CASIZ, Type Series No. 703), together with 6 paratypes (CASIZ, Type Series Nos. 704). Color slides of the type material are at CASIZ, Color Slide Series. Paratypes have also been deposited with the Los Angeles County Museum of Natural History (LACM 1857), San

Diego Museum of Natural History (SDNH 68728), United States National Museum of Natural History (USNM 770960), Academy of Natural Sciences, Philadelphia (ANSP A7226), and the American Museum of Natural History (AMNH 183855).

Type Locality: Northeast Anchorage (29°11'N; 118°17'W), Guadalupe Island, Baja California, Mexico, where 4 specimens, including the here designated holotype, were collected, December 30, 1974, by Dr. Welton L. Lee and myself.

Distribution: In addition to the 2 type lots mentioned above, the following collections came to my attention, all from Guadalupe Island: CASIZ 32746, intertidal, stas. M-25-A & M-25-C, south end of Guadalupe Id., *leg.* M. Woodbridge Williams, July 1946, [misidentified as *Lepidozона mertensii*] 27 specimens; SDNH 9957, *leg.* C. L. Hubbs *et al.* [misidentified as *L. mertensii*] 2 specimens; LACM 65-41, at 20 feet [6 m], West Anchorage (28°58.5' N; 118°18' W), *leg.* L. Thomas & B. Owen, Oct. 1975, 22 specimens; LACM-AHF 1912-49, intertidal, Melpomene Cove (28°52'05" N, 118°19'05" W), Dec. 17, 1949, 1 specimen; LACM-AHF 1293-49, intertidal, 2½ miles [4 km] north of South Bluff (28°54' N; 118°16' W), Dec. 19, 1949, 2 specimens; LACM-AHF 1925-49, 35 - 40 fathoms [54 - 73 m], 2½ miles [4 km] from South Bluff (28°53'44" N; 118°15'35" W), Dec. 20, 1949, 2 specimens. From these collections, it seems that the species is endemic to Guadalupe Island, and has a bathymetric range from intertidal to about 70 m.

Individual Variation: *Lepidozона guadalupensis* displays only moderate variation in color; the pinks and the browns predominate, often in a variegated combination where some splashes of white may also be seen. A common color pattern is that of blotches of dark brown along the pleural areas on a rose-pink background. The double (or single) transversal bands of light color so commonly seen in *L. mertensii* were not observed in any of the specimens examined.

In size, *Lepidozона guadalupensis* seems to be smaller on average than its sibling species, *L. mertensii*. The largest specimen of *L. guadalupensis* measures, including girdle, 31.0 mm in length (CASIZ 32746). Variations in other meristic characteristics are summarized in Table 1.

Remarks: *Lepidozона guadalupensis* bears a very close resemblance to *L. mertensii* with which it could be easily confused. However, the 2 species differ in their average size, general color, the presence (or absence) of sulci defining the radial ribs on the end valves and lateral areas, and the ornamentations of the girdle scales. Still, their resemblance is such that, at one point in this study, the

appropriateness of making *L. guadalupensis* simply a subspecies of *L. mertensii* was seriously considered.

In its relatively remote position, Guadalupe Island is a true oceanic island that has never been connected with other shores; it is the top of a volcanic mountain that rises some 3600 m from the surrounding ocean floor. It is tempting to speculate that *L. guadalupensis* evolved from *L. mertensii* under the conditions of geographic isolation that characterize Guadalupe Island. But while the larvae of *L. mertensii*, having reached the Island from the Mainland, evolved and speciated into *L. guadalupensis*, it is intriguing to realize that a similar phenomenon of differentiation and speciation did not affect other species which reached Guadalupe Island by similar means, and conceivably at the same time. Populations of *Cyanoplax hartwegii* (Carpenter, 1855), *Callistochiton palmulatus* Dall, 1879, and *Nuttallina californica* (Reeve, 1847) among others (A. G. SMITH, 1963) known on the Island remain identical to their stocks of origin on the Mainland.

Radiometric dating places the age of Guadalupe Island at about 7 million years (HUBBS, 1967), and so fixes the maximum age of *Lepidozона guadalupensis*.

Fossil Record: In pleistocene material from Guadalupe Island made available to me through the courtesy of Dave R. Lindberg and Barry Roth, California Academy of Sciences, I have identified three intermediate valves of the species here described as *Lepidozона guadalupensis*. In the same deposit, 3 valves of *Nuttallina californica*, and 1 valve of *Callistochiton palmulatus* were also found. Corals from this deposit (SDNH Loc. # 0641: coquina sample taken from E side near south end of Islote Negro, on west coast of Guadalupe Island, at about 3 to 6 m above sea level, C. L. Hubbs, April 19, 1957) have been radiometrically dated at between 110,000 and 130,000 years before present (GOLDBERG, 1965).

Discussion

A number of other eastern Pacific species of chitons have been referred, albeit tentatively, to the genus *Lepidozона*:

Ischnochiton stearnsii Dall, 1902: Holotype (USNM 109024), collected off Farallon Islands, California, in 391 fathoms [715 m] was examined thanks to the courtesy of Dr. Joseph Rosewater. Another specimen (LACM 65-4), off Catalina Island, California, 250 fathoms [475 m] was examined through the generosity of Dr. James H. McLean. Recently, the study of material in the collection of the Allan Hancock Foundation, now at the Los Angeles Museum of Natural History, revealed two more specimens of *I. stearnsii*, one off San Clemente Island, 250 - 300 fathoms [475 - 549 m] (LACM-AHF 1019-39), another

found near Catalina Island, in 240-250 fathoms [439-457 m] (LACM-AHF 2004-50). The presence of 2 slits in some of the intermediate valves, and the spiculoid girdle scales exclude *I. stearnsii* from *Lepidozonia*. The species appears to belong to the same species-group as *I. abyssicola* A. G. Smith & Cowan, 1966, and perhaps *I. acelidotus* Dall, 1919 [= *I. exanthematus* Dall, 1919] as suggested by A. G. SMITH & COWAN (1966: 14-15), and A. G. SMITH (1977: 218-219). Whether or not a new genus may have to be erected to accommodate these species is a matter for future consideration. Color slides of the holotype of *I. stearnsii* at CASIZ, Nos. 1030-33, 1046, 1070, 2050-51 (A. G. Smith), and 3120-22 (AJF).

Ischnochiton (Lepidozonia) asthenes Berry, 1919: Collected intertidally at White's Point (Type locality), Los Angeles County, California (CASG 439180), Coronados Islands (SDNH 53867), and Guadalupe Island (CASG 32746) Mexico, the species belongs in the genus *Callistochiton* Dall, 1879, on account of the bicostate lateral areas, radial undulations (instead of "ribs") of the end valves and lateral areas, minute girdle scales and slits that correspond in number and position to the undulations of the tegmentum.

Ischnochiton veredentiens Carpenter, 1864: Holotype (USNM 16259), from "Catalina Island", California, examined through the courtesy of Dr. Joseph Rosewater, is reduced to only 6 disarticulated valves (to which bits of glue adhere) and dried soft parts. The girdle is missing. The lateral areas have two granulose radial ribs; the central areas, longitudinal riblets, latticed. The mucro is central. This small specimen (perhaps 6 to 7 mm long, if intact) looks like a member of the genus *Lepidozonia*. Although I am inclined to the belief that the specimen is a juvenile of *Lepidozonia sinudentata*, species assignment is unwarranted, under the circumstances, and the name should be considered as a *nomen inquirendum* (A. G. SMITH, 1977: 216, 238). Color slides of the holotype are CASIZ, Nos. 2978 (A. G. Smith), and 3125 (AJF).

Ischnochiton (Ischnochiton) newcombi Carpenter in Pilsbry, 1892: Holotype (Redpath Museum no. 19) examined through the generosity of Dr. Vincent Condé. This is a small specimen (about 9 mm long) whose valves i, vii, viii are broken into small but still identifiable fragments. Central areas have a granular surface; lateral areas have some 4 radial ribs bearing coarse, irregular, low tubercles. As PILSBRY (1892: 120) noted, the specimen "resembles that of *I. interstinctus* though coarser and different in detail." Although not a likely member of the genus *Lepidozonia*, the species must be regarded for the moment as valid (A. G. SMITH, 1977: 228-229). Color slides, CASIZ, Nos. 3089-91 (A. G. Smith), and 3083-85 (AJF).

The genus *Lepidozonia* seems to be confined to the north Pacific. It is not reported in the Caribbean (KAAS, 1972), in the Mediterranean (SABELLI, 1974), or other European waters (Richard Van Belle, *in litt.* March 23, 1975). On the other hand, the list of Japanese species is long: *Lepidozonia coreanica* (Reeve, 1847) [= *L. pectinella* Bergenhayn, 1933, *vide* ISAO TAKI, 1938]; *L. iyoensis* (Is. Taki & Iw. Taki, 1929); *L. amabilis* (Berry, 1917); *L. interfossa* (Berry, 1917); *L. sahlini* Bergenhayn, 1933; *L. pallida* Bergenhayn, 1933. Although I have had no opportunity of examining representatives of most of these species, it seems from the descriptions given that these may in fact belong to the genus *Lepidozonia*. All of these nominal species have uni-slitted intermediate valves.

However, another group of North Pacific species often referred to *Lepidozonia* should be given a different generic assignment on account of their radsioid, i.e., two-slitted intermediate valves: *Chiton albrechti* Schrenck, 1867; *Ischnochiton (Lepidozonia) nipponica* Berry, 1918 [new name for *Ischnochiton (Lepidozonia) pilsbryanus* Berry, 1917 (not *Ischnochiton pilsbryanus* Bednall, 1896); = *Lepidozonia pilsbryana* Is. Taki, 1938; *Ischnochiton (Lepidozonia) berryanus* Leloup, 1941]; *Ischnochiton bisculptus* Carpenter in Pilsbry, 1892 [considered uni-slitted by Pilsbry (1892: 119) but found to be two-slitted by Leloup (1941: 5)]; *Gurjanovillia lindberghi* Jakovleva, 1952 [= *G. derjugini* Jakovleva, 1952, *vide* Sirenko, 1975]; *Lepidozonia multigranosa* Sirenko, 1975; *Lepidozonia thielei* Sirenko, 1975; *Lepidozonia ima* Sirenko, 1975. The appropriate generic assignment of these species cannot be decided at this time. Conceivably, they may be referred to the genus *Gurjanovillia* Jakovleva, 1952, now removed from the synonymy of *Lepidozonia* Pilsbry, 1892 (FERREIRA, 1977: 28-29). The matter awaits further study.

In the Indo-Pacific the genus *Lepidozonia* is not known, except perhaps for one species from the Java Sea, *Callistochiton finschi* Thiele, 1910 [= *C. recens* Thiele, 1911] which IREDALE & HULL (1925, 4: 354-355) referred to the genus *Solivaga* Iredale & Hull, 1925, now synonymized under *Lepidozonia* (A. G. SMITH, 1960; FERREIRA, 1974).

In the eastern Pacific, 14 species of *Lepidozonia* are now recognized, 6 from the Tropical Region (FERREIRA, 1974), and 8, herein, from the northern Temperate Region. Whether the genus *Lepidozonia* is present (or absent) from the southern Temperate Region of the eastern Pacific is an open question pending better knowledge of the South American fauna. It is not known in the Galápagos Islands (A. G. SMITH & FERREIRA, 1977).

The geographic range of the eastern Pacific species of *Lepidozonia*, as presently known, is summarized graphically in Diagram 1 which illustrates well the faunal break known to occur at about Magdalena Bay in Baja Califor-

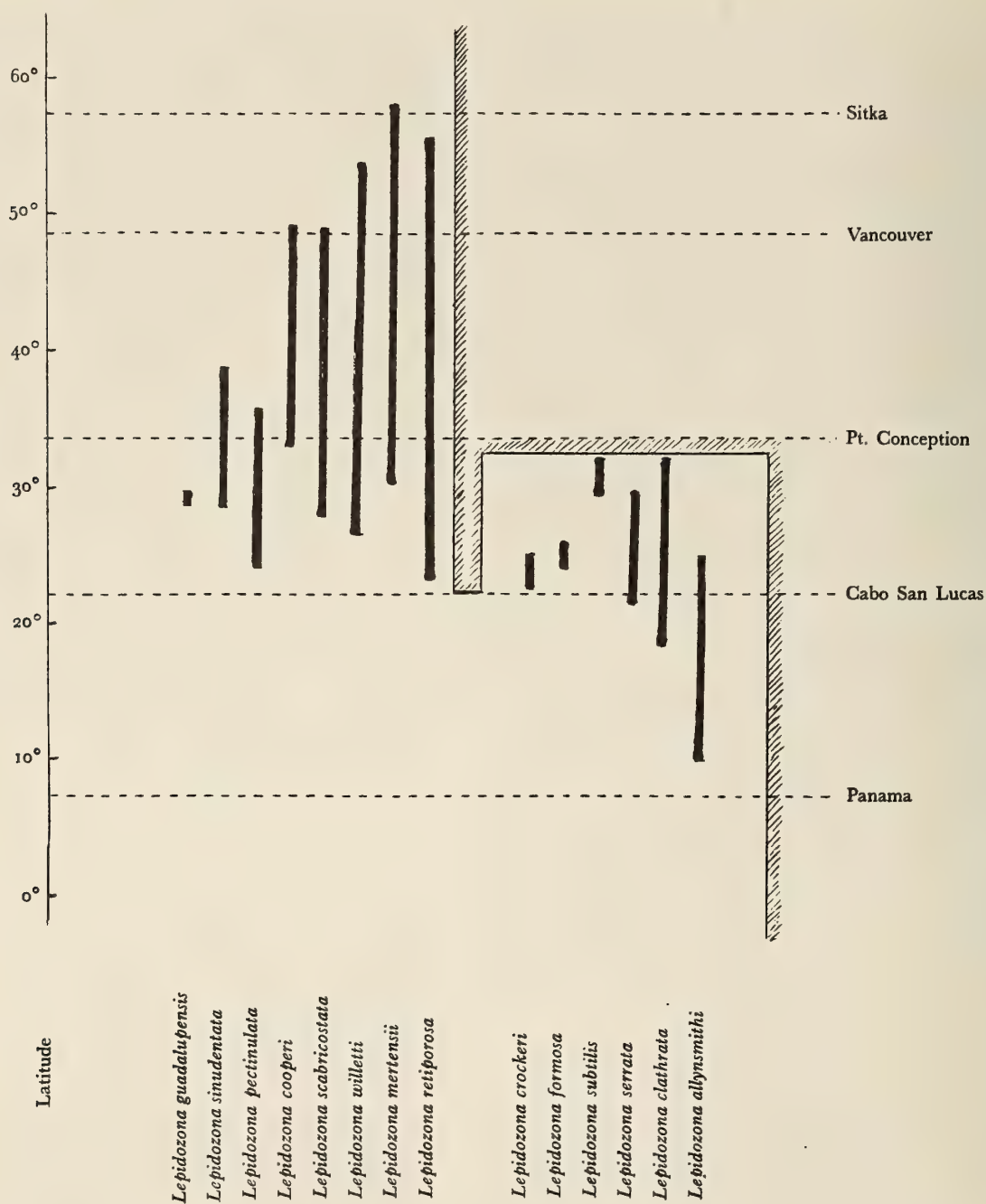


Diagram 1

Geographical Distribution of the Species of *Lepidozона* Pilsbry, 1892
in the Northeastern Pacific

nia (BRIGGS, 1974). *Lepidozona serrata* (Carpenter, 1864) has been collected at Magdalena Bay, Baja California (leg. H. N. LOWE, December 1931, SDNHM 23622), San Diego (DALL, 1921), and Monterey Bay, California (FERREIRA, 1974); but these findings seem to be freakish events which have remained uncorroborated by the same or other collectors. Thus, *Lepidozona serrata* cannot be considered a normal component of the chiton fauna of the North Temperate Eastern Pacific.

It is worth noting that, in this work, the study of the radula proved to be very unproductive. Despite the promises embodied in the works of THIELE (1893), JAKOVLEVA (1952) and others, in my experience the radula of chitons has not yielded significant means of distinguishing most species, genera, or even families. This is certainly the case with the species of *Lepidozona* in this study whose radulae are, except for size, practically identical. Thus, to avoid uninformative redundancy, only the radula of *L. merten-sii* is illustrated (Figure 34).

By contrast, the study of the girdle scales, greatly improved by the advent of SEM microphotographs, has provided most valuable information. As a taxonomic character, among all the features that distinguish the individual species of *Lepidozona*, the girdle scales have appeared most reliable for their uniqueness and constancy. Even in the case of juvenile specimens, much before the appearance of characteristic tegmental sculpture, the girdle scales can lead, often with assurance, to the identification of the species in question.

The particular significance of the girdle scales in *Lepidozona* was anticipated by PILSBRY (1893) with the suggestion of two groupings, the *L. merten-sii* group of species with strongly convex, mostly smooth, nipples scales, and the *L. coreanica* group of species with flattish, striated scales. Within this scheme, a phylogenetic tree of the species of *Lepidozona* in the North Temperate Region of the eastern Pacific is proposed in Diagram 2 (cf. FERREIRA, 1974).

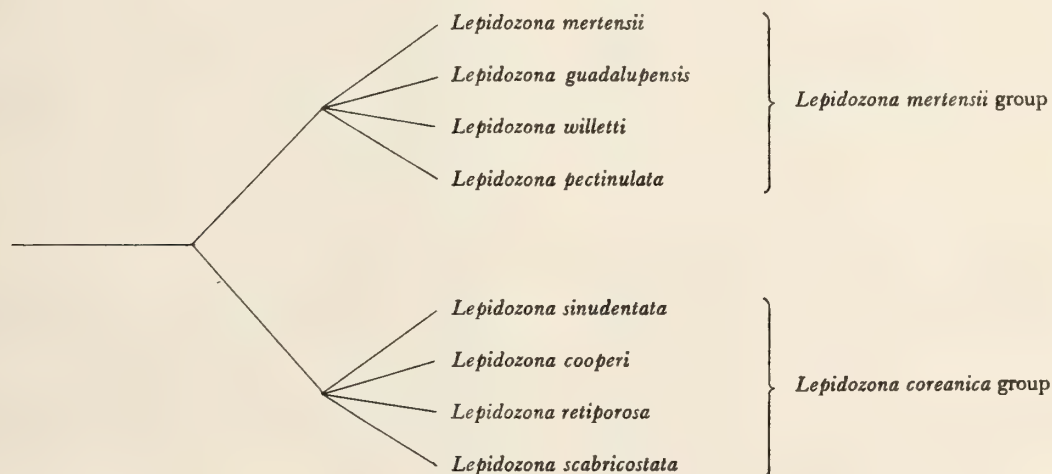


Diagram 2

Tentative Phylogenetic Tree of the Genus *Lepidozona* Pilsbry, 1892,
in the North Temperate Region of the Eastern Pacific

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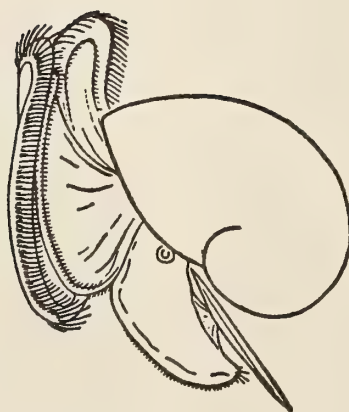
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Wharf Piling Fauna and Flora in Monterey Harbor, California

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(1 Plate; 10 Text figures)

INTRODUCTION

ON THE WEST COAST of the United States few studies have been made on the identity and distribution of wharf piling dwellers except for investigations associated with the destructive effects on wooden piles of shipworms and gribbles. RICKETTS (see first edition of RICKETTS & CALVIN, 1939) was one of the first investigators to look critically at the organisms living on piles along the Pacific coast. He observed the different populations on piles in protected harbors as contrasted to those under piers on the open coast, and noted that, although there was a general intertidal zonation of plants and animals on the piles, this zonation was not as sharp and well-defined as that observed on the Atlantic coast. Ricketts paid particular attention to wharf piling dwellers in Monterey Harbor and in the late 1920s and early 1930s observed the initial colonization of the piles under a newly constructed wharf. In the intervening years a number of investigators, mainly students and staff from Hopkins Marine Station, have made observations on and have collected animals and plants from various harbor pilings. Also, since 1965, investigators from the Naval Postgraduate School have conducted long-term fouling studies in the harbor, and in 1968, LANG, as part of a student SCUBA project, did a photographic survey of the most common plants and animals dwelling subtidally on the piles. The settlement and growth of sessile marine invertebrates on experimental piles in the harbor was investigated by HADERLIE (1974).

Monterey has been a port since 1602 when it was established as the center of Spanish California. The first substantial wharf to be built on the Pacific coast was constructed at Monterey in 1845. Following this, during the height of the California whaling industry in the 1870s and the sardine fishery following World War I, a number of wharfs using wooden pilings were built and rebuilt. The only surviving wharf of this group is the one now known as Fisherman's Wharf which has been repaired constantly by replacing piles. It had been recognized for

many years that a more substantial, permanent wharf was needed, not only to serve the fishing fleet but also to facilitate the unloading of cargo, particularly lumber, from ocean-going ships. In 1926 plans were drawn for a major new wharf and construction begun. The new wharf, completed in 1927, is now known as Monterey Municipal Wharf No. 2. In the late 1920s Ricketts made collections from the concrete and wooden piles supporting this wharf. As of now, some of the piles have been in the water for 50 years and carry a massive aggregation of organisms. The variety and biomass of the growth on these piles equal or exceed those found on the rocky shore nearby, yet, until this present investigation, the piles had not been subjected to qualitative and quantitative biological scrutiny.

In 1974 a detailed study was initiated on the piles and sea walls of Municipal Wharf No. 2. It was immediately obvious that no two piles carried the same population of organisms. Indeed, some piles carried populations quite distinct from others. Piles at the distal end of the wharf are colonized, in general, with organisms tolerant of wave shock, for the end of the wharf is exposed. Organisms on the piles at the shoreward end of the wharf are those characteristic of quiet harbor water.

For this study we have looked at the intertidal growth on most of the piles and recorded the major organisms that are obvious to the naked eye. We have also made a similar survey of the sea walls associated with the wharf. Using SCUBA we have examined and recorded the major subtidal organisms from both wooden and concrete piles along the length of the wharf. In the 3 years this study has been in progress we have also had the opportunity to examine 25 wooden fender piles, some having been in place 20 years or more, which have been removed and replaced. These gross observations gave us some idea of the diversity and density of living organisms on the piles from various parts of the wharf. To gain detailed knowledge regarding the numbers and kinds of wharf piling dwellers we realized we would have to remove totally

the mass of organisms down to the substrate and make a detailed laboratory analysis of the collection. For this detailed study we selected 4 concrete piles in one row under the main wharf which seemed to be fairly representative of the wharf as a whole. We had intended to subject each of these 4 piles to detailed study from above the high water line to the sediment line at the bottom. We were able to complete the analysis for the intertidal organisms on all 4 piles. The subtidal survey proved so laborious and the laboratory work so time consuming, however, that only one of the 4 piles was completely analyzed. This paper is an attempt to summarize what we have learned. The detailed subtidal work resulted in a master's thesis (DONAT, 1975), and a preliminary report on the intertidal work has been published (HADERLIE, 1977).

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AREA OF STUDY:

Description of Monterey Municipal Wharf No. 2

Figure 1 includes a vicinity map and shows the present configuration of Monterey Harbor. Figure 4 is an aerial photograph of the harbor and adjacent area of Monterey Bay. Figure 2 presents a plan view of Monterey Municipal Wharf No. 2. This wharf has its footing on the sandy shore at the base of Figueroa Street in Monterey and extends northward into the bay for approximately 530 m. At the distal end of the wharf the water is 8 to 10 m deep. The initial part of the structure is a causeway 10 m wide running seaward for 341 m. It is supported by wooden piles approximately 30 cm in diameter. The piles are in 80 rows of 6 piles each, each row 4.27 m apart. The causeway piles out to the position of the north sea wall (see below) are encased in concrete jackets to about 1 m above the highest tide level. Beyond the causeway for a distance

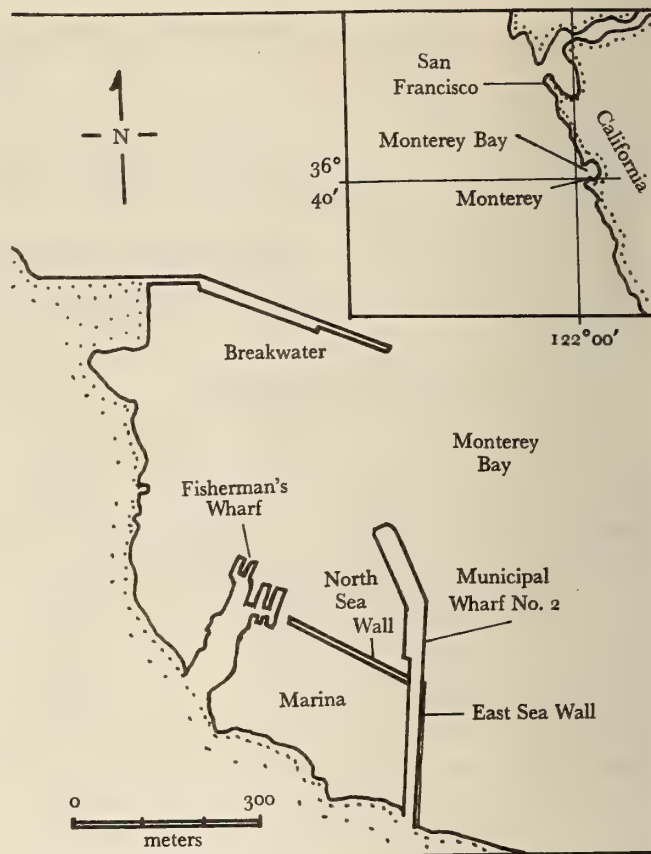


Figure 1

Map Showing Configuration of Monterey Harbor

of 57 m the section is called the lumber wharf. It is 18 m wide and supported by 14 rows of wooden piles, 10 piles per row, the rows 4.27 m apart. The section beyond the lumber wharf is called the main wharf. It is 25.7 m wide, 128 m long, and is supported by 36 rows of concrete piles, the rows 3.65 m apart and containing 12 piles. The main wharf accommodates a large building that houses fish processing plants.

The basic configuration of the wharf has remained the same since its construction but over the years additions and alterations have been made. To protect the wharf

(on facing page →)

Figure 4: Aerial photograph of Monterey Harbor (17 September 1971, official U.S. Navy photograph by VC-63 squadron NAS Miramar)



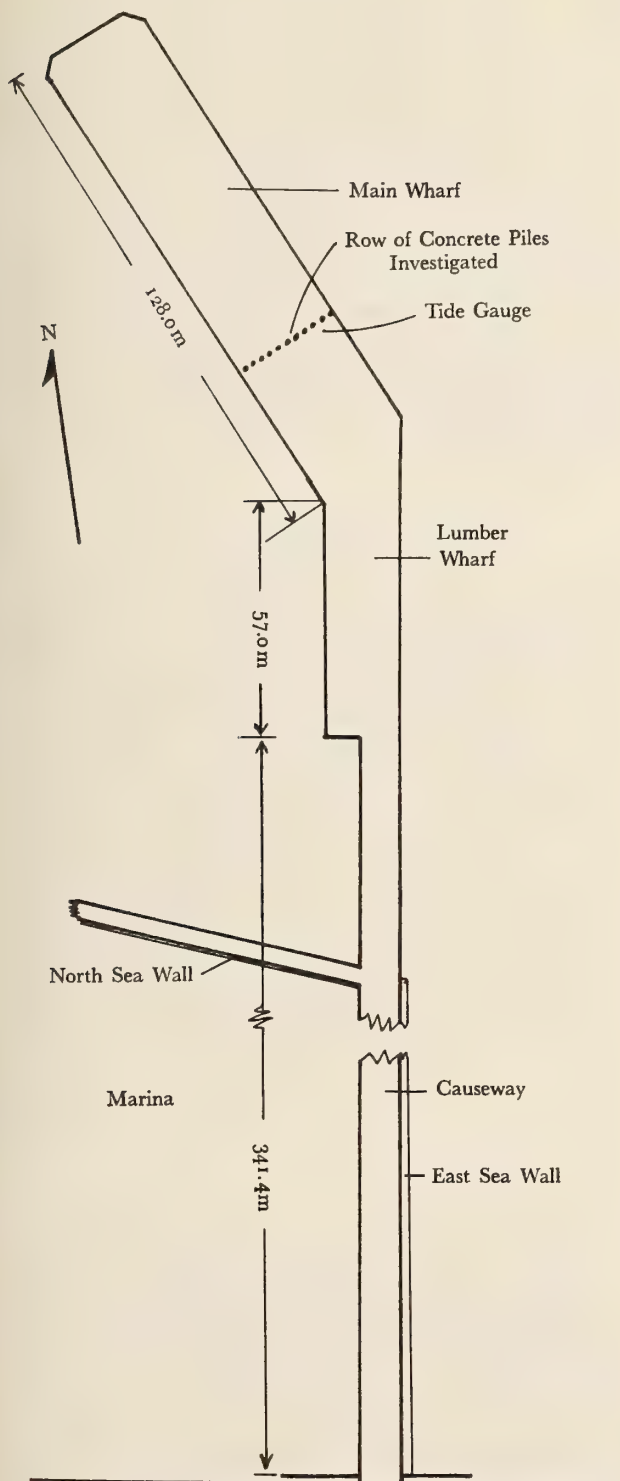


Figure 2

Monterey Municipal Wharf No. 2

structure from damage by large fishing boats and ships moored during periods of strong surge, a series of wooden fender piles were driven around the entire periphery of the wharf, normally one fender pile at each end of each row of supporting piles. Because of wear these wooden fender piles are removed and replaced periodically. All wooden piles used in the wharf construction and repair have been Class A Douglas fir pressure treated with 6.3 kg creosote according to standards of the American Wood-Preserver's Association. They vary in diameter from 25 to 35 cm.

Each concrete pile under the main part of the wharf is octagonal in cross-section, approximately 2 m in circumference (61 cm diameter) and extends from the base of the wharf deck 5 m above mean lower low water (MLLW) to the bottom 7–8 m below MLLW. The piles were poured in forms on land, and were made of steel reinforced concrete using portland cement and a good quality granite aggregate. They were then driven in place and capped with concrete beams. Most of the concrete, both above and below the water, is in excellent condition after 50 years, however, there is evidence that many of the steel reinforcing rods have corroded away.

Monterey is situated at the southern end of Monterey Bay which is broadly open to the Pacific to the west. It is not a natural harbor and is particularly exposed to waves and swell from the northwest. To give some protection to the wharfs in the harbor, and to the mooring area of the large fishing fleet that became permanently home-ported at Monterey in the 1920s, an extensive permeable breakwater consisting of granite rock was constructed by the U.S. Army Corps of Engineers between 1931 and 1934. The position of this breakwater is shown in Figure 1 and Figure 4. The breakwater gives considerable wave protection to Municipal Wharf No. 2, but does not alter significantly the water circulation in the area of the wharf itself.

In 1959–60 a major addition to the harbor and wharf was made. To accommodate an ever increasing number of fishing boats and pleasure craft, a marina with floating docks was constructed between Municipal Wharf No. 2 and the older Fisherman's Wharf. Figure 4 shows the configuration of the marina. To gain the quiet water necessary for a marina, a sea wall was built between the two wharfs with a narrow passageway near Fisherman's Wharf allowing boats to enter and leave the marina. This sea wall, known as the north sea wall or frontal wall, is constructed of braced pilings with heavy wooden planks (20 × 30 cm in section) forming a nearly impermeable barrier from above high water line to the bottom. A fishing pier has been built on top of the sea wall. To protect the marina from the accumulation of sand caused by lit-

toral drift from east to west, and to give additional protection from waves and surge from the open bay, a sea wall was also constructed along the east side of the causeway of Municipal Wharf No. 2 out to the level of the north sea wall. This so-called east sea wall was constructed adjacent to the east side of the causeway of additional fender piles with heavy wooden planking (15×30 cm) forming an impermeable barrier. Additional wooden piles were driven diagonally into the bottom to the east of the sea wall to brace the entire structure. To the west of the marina the extensive piling under Fisherman's Wharf dampens any wave action from that direction. The only major unobstructed opening into the marina is the passageway for boats, therefore no significant wave action occurs and the currents within the marina are primarily tidal currents. As a result of the construction of the marina, the fauna and flora on the now enclosed piles of the causeway have been altered significantly as will be noted below.

ENVIRONMENTAL PARAMETERS

For many years the Naval Postgraduate School has operated a tide gauge on the wharf near the main study site of this investigation. Using the original blueprint of the wharf as drawn in 1926, the tide gauge is located near pile J, Bent 11. Its position is shown in Figure 2. At this same site, daily surface temperatures are recorded and, at times, bottom water temperatures. Salinity determinations are also made periodically. The detailed records are maintained by the Department of Oceanography, and those of specific years have been summarized by DONAT (1975), HADERLIE (1968, 1969, 1974) and HADERLIE & MELLOR (1973). Only an over-all summary of these records will be given here.

The maximum spring tidal fluctuation in Monterey Harbor is about 2.7 m; from 2.2 m above mean lower low water (MLLW, defined as 0.0 m tide level) to 0.5 m below MLLW. Between 1966 and 1977 the highest surface temperature (17.4°C) was recorded in September 1968, and the lowest (9.5°C) in March 1971. The average low temperature over the past 10 years has been $11-12^{\circ}\text{C}$ and the average high, $15-16^{\circ}\text{C}$. In most years there is a general upward trend in surface temperature from January to September, with a sharp decline from September through December. The surface salinity of harbor water for the past several years (when averaged monthly) ranged from 32.8‰ to 33.8‰ . Water under that part of the wharf seaward of the north sea wall of the marina circulates freely and at times strong tidal currents and surges

occur. The water is well aerated and relatively unpolluted. The piles under the causeway to the east of the marina, however, are in relatively quiet water subject to minimal currents and the water in this area is somewhat polluted, especially by oil spills from boats moored in the marina. No detailed temperature and salinity records have been maintained for the marina area. The sea bottom under the wharf consists of fine sand and sediment with a mean grain diameter between 0.25 and 0.125 mm. Direct sunlight irradiates the piles on the eastern side of the wharf for a few hours in the morning; piles on the western side are subject to direct sunlight for longer periods in the afternoon. Some direct sunlight reaches the piles near the middle of each row only in late afternoon and the general dim light conditions limit the number of plants in this area.

METHODS

Municipal Wharf No. 2 is supported by about 1,300 piles. Over the past 10 years most of these have been examined, some fairly casually, a few in considerable detail. Depending upon the detail of examination, the methods varied. As a whole two routines were followed. In what we will call our general survey, many piles and the sea walls were grossly examined to determine the dominant kinds of organisms in each area and their relative abundance and vertical distribution on the pile or portion of the sea wall. Except to confirm the identity of species, no extensive collections of organisms were made. For a few concrete piles, however, we made a detailed survey where all organisms on one face of the pile were removed, the biomass of each vertical segment determined, and a detailed species count made. Each of these two types of survey methods will be discussed in more detail.

A. GENERAL SURVEY

a. Intertidal Area

In the intertidal zone at the shoreward end of the causeway the piles and east sea wall were examined at low tide on foot. For the remainder of the sea wall and piles out to the end of the wharf small boats and rafts were used. Surveys were made at low tide (0.0 m or lower) and the piles and sea wall were examined from -0.5 m tidal level to the highest reaches of the tide. The general distribution and abundance of all macroscopic, easily identifiable plants and animals were noted.

b. Subtidal Area

For subtidal work SCUBA gear was used. A weighted line, marked off in 0.5 m increments was deployed along each pile being studied and a census was made using underwater slates. Approximately 20 representative wooden piles and 10 concrete piles were surveyed. Some photographs were taken of specific sections of piles, but, in general, detailed photography was limited to the concrete pile studied in the detailed survey (see below). During 1976 and 1977 approximately 30 wooden piles were pulled and replaced by the Harbor Maintenance Supervisor, and 25 of the removed piles were examined immediately after they were lifted from the water with a census made and vertical distribution of organisms determined.

B. DETAILED SURVEY

It was recognized early in this study that a detailed analysis of the fauna and flora on the various piles under the wharf was needed. Yet our general survey indicated that there were often great differences from pile to pile. We could not possibly perform a detailed analysis on more than a few piles; thus, it was desirable to select piles that were fairly representative of those under the wharf in that each carried a somewhat different population representing the range found on all the piles. We ultimately settled on 4 concrete piles in a single row under the main part of the wharf. The specific piles selected for study are in the 25th row from the end of the wharf—one at the eastern edge of the row (designated Pile A), 2 near the middle (Piles B and C) and one near the western edge of the row (Pile D). The general position of the row is indicated in Figure 2, and Figure 3 shows a cross-section of the wharf with the specific piles labelled. On the orig-

inal 1926 blueprint of the wharf filed in the City Engineer's Office, City of Monterey, Piles A, B, C and D are designated L, J, F and B, Bent 12.

a. Intertidal Area

In order to gain continual access to the piles being studied a series of cat-walks were constructed along the row of piles. Ladders suspended from the cat-walks and extending to below the lowest tide level were placed adjacent to each study pile. Small boats and rafts were also employed. After an initial survey of the organisms attached in the intertidal zone on each of the four piles was completed, and before any of the attached fouling growth was removed, a photograph was taken of each 0.5 m segment of each pile. The fouling growth around the periphery of any one pile at a specific level proved to be much the same, i.e., the north face of the pile carried the same organisms in about the same concentrations as the south face. It was decided, therefore, to study only one side of each of the four piles—the south side—and leave the north side undisturbed for later reference. Each pile has a circumference of 2 m, therefore, a 1 m swath from high to low water on the south face of each of the four piles was investigated.

After the initial census and photographic recordings were made, the south face of each pile was scraped completely clean of all macroscopic fouling growth. This was done in 0.5 m vertical increments, thus, each increment was 1 m wide and 0.5 m high. The organisms were removed from the piles using various scrapers and chisels and were caught by an elastic apron attached around the pile below the area being scraped. The collected fouling growth from each 0.5 m² increment of pile surface was placed in buckets of sea water and taken immediately to the laboratory where all the removed organisms, after pouring off the water, were weighed (wet weight of all fouling growth for 0.5 m² of pile). The organisms were then sorted in pans of fresh sea water, identified and counted. In most cases all organisms were identified while still alive, but for some polychaetes the specimens were preserved in alcohol for later identification. An attempt was made to identify and count all organisms visible to the unaided eye, but on some piles with entangled masses of worm tubes many small organisms were obviously missed. Attempts to count and quantify colonial organisms such as hydroids and encrusting bryozoans were especially frustrating. A stereoscopic microscope was used to identify the smaller animals and plants.

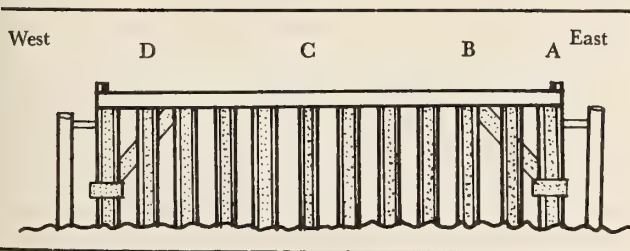


Figure 3

Section Through Wharf at Level of Concrete Piles Investigated

b. Subtidal Area

As noted above, our initial general survey of the wharf piles indicated that there were considerable differences from pile to pile in the populations of fouling organisms. This was especially true in the intertidal region of each pile. The subtidal region of the piles carried a somewhat more uniform population. The 4 concrete piles selected for detailed study were fairly representative of the wharf piles as a whole in the range of organisms living on them. We had intended to make a detailed study of the subtidal populations on all 4 of the selected piles, as had been done for the intertidal populations. The collection and analysis proved to be so time consuming and laborious, however, that we finally decided to make a general survey, including an extensive photographic record, of the subtidal region of each of the 4 piles and concentrate for the detailed study on only one, Pile A.

During the spring and summer of 1974 a total of 8 dives was made on the 4 piles to make a general census and a photographic survey and to test collecting methods and equipment. During the fall of 1974 and up to July 1975 a series of 13 dives was made in the detailed study and collection of organisms from Pile A. Two to 3 divers participated in each dive.

Photographic records were made using a Nikonos II underwater camera with a Nikkor wide-angle lens (1:3.5, f28) and a Subsea Products MK 150 underwater flash attachment. Kodak High Speed Ektachrome (ASA-160) was used for color slides and Kodak Tri-X (ASA-400) was used for black and white (see DONAT (1975) for details on underwater photography). A complete file of photographs of organisms living on the piles of the wharf is maintained by the Department of Oceanography, Naval Postgraduate School.

As in the intertidal region of Pile A, the organisms from the south face of the pile from the -0.5 m tide level down to the bottom at -7.0 m were removed and collected. A swath 1 m wide was scraped in 0.5 m vertical increments as in the intertidal area. A weighted line marked off in 0.5 m segments was placed next to the pile during each collective dive. The primary tools for removing the organisms consisted of a steel chisel 18 cm long with an 8 cm blade width and a small 1.6 kg sledge hammer.

Collection of material beyond reach when standing on the bottom necessitated the use of diving stages on which the diver could stand or kneel while working on the pile. These stages were secured above the water line to the adjacent cat-walk and raised or lowered to the correct position. A girdle line passed around the pile about 1 m below the level of material to be collected gave adequate stability for the work.

A collection bag was improvised from an old plankton net 1.5 m long with a 0.5 m diameter opening. A line around the pile kept the lower lip of the bag against the pile face and the upper lip was held at a slight angle to the pile. A slow sweeping motion of the hand down into the bag opening carried the falling material that was scraped loose into the bag with negligible loss. Upon completion of scraping a 0.5 m² increment the bag was removed and taken to the surface. The collected material from each 0.5 m² increment was taken directly to the laboratory, drained of all excess water, and weighed. The organisms were then placed in aquaria or porcelain pans with running sea water until they were all sorted and either identified while alive or preserved in alcohol for later identification. In the initial sorting of the collection the numerous plumose anemones (*Metridium senile*) were removed as soon as possible, for their protruding acontia fouled and killed many small organisms.

OBSERVATIONS

a. Fauna and Flora of Piles and East Sea Wall of Causeway

Prior to 1959, when the marina was developed, the piles under the causeway were in open water and subject to the same tidal currents and surge as the piles under the outer part of the wharf. The animals and plants living on these causeway piles were similar in kinds and numbers to those found elsewhere on the wharf. Construction of the practically impermeable wooden sea wall along the eastern side of the causeway and the connecting north sea wall created a partially enclosed and protected area for the marina and drastically altered the water movements around the piles under the shoreward part of the causeway. As a result, the fouling growth on these piles is now impoverished. The remaining organisms are those tolerant of quiet harbor water that is often polluted, especially by oil spills.

Subtidally, the enclosed piles of the causeway carry reasonably heavy growths of the tube worms *Phyllochaetopterus prolifica*, the plumose anemones *Metridium senile*, and numbers of hydroids, erect bryozoans, and stalked tunicates (*Styela montereyensis*). In the low intertidal zone, very few living giant barnacles (*Balanus nubilus*) are now found, whereas they were common before the sea wall was constructed. The entire intertidal area on each pile now carries a very limited population of smaller barnacles (*Balanus glandula*, *Chthamalus dalli*, *Tetraclita squamosa rubescens*) and anemones (*Anthopleura elegantissima*, *Corynactis californica*).

The intertidal area of the sea wall itself on the protected marina side is inhabited by many of the same animals observed on the adjacent protected piles, but, in addition, possesses patches of ascidians (*Ascidia ceretodes*, *Botryllus* spp.), small *Metridium senile*, and a few patches of *Corynactis californica*. Also, extensive growths of the encrusting bryozoans *Celleporaria brunnea* and *Cryptosula palasiana* occur as well as the erect bryozoans *Bugula neritina* and *Crisulipora occidentalis*. In areas where the planks of the sea wall have separated slightly producing a crack through which sea water can flow, the opening is often lined with clumps of the stalked barnacle *Pollicipes polymerus* and the bay mussel *Mytilus edulis*.

To the east of the causeway the sea wall is supported by bracing wooden piles driven at an angle of 60° to the vertical. These piles and the east face of the sea wall are exposed to the open water of the bay and to full sunlight for several hours each day, and they are populated by a great variety of plants and animals. No attempt has been made to make a detailed survey of these organisms, but the dominant forms that can be seen in a casual inspection of the intertidal area of the piles and sea wall will be mentioned.

Lush growths of marine algae occur on the east face of the sea wall. High up at the level of the highest tide is a green band of *Enteromorpha compressa* (Linnaeus) Greville, 1830. Slightly below, *Ulva lobata* (Kützinger) Setchell & Gardner, 1920, dominates the sea wall and extends downward to mid-tide level. Mixed with the *Ulva* is the filamentous green alga *Urospora penicilliformis* (Roth) Areschoug, 1886, and the red alga *Porphyra lanceolata* (Setchell & Hus) Smith, 1943. The mid-intertidal region of the sea wall is populated with well-separated plants consisting primarily of *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1820, *Gigartina exasperata* Harvey & Bailey, 1851, and *Cystoseira osmundacea* (Turner) C. Agardh, 1820. The low intertidal zone is dominated by red algae including *Polyneura latissima* (Harvey) Kylin, 1924, *Pterosiphonia dendroidea* (Montagne) Falkenberg, 1901, *Iridaea cordata* (Turner) Bory, 1826, and by larger brown algae including *Dictyoneuropsis reticulata* (Saunders) Smith, 1942, and *Desmarestia lingulata* (Lightfoot) Lamouroux, 1813.

The animals inhabiting the east face of the sea wall are not as dense as on the adjacent bracing piles. High in the intertidal area *Balanus glandula*, *Pollicipes polymerus* and small individual *Mytilus edulis* are common. Some small *Mytilus californianus* inhabit crevices. In the mid-intertidal zone *Anthopleura elegantissima* dominates the sea wall, with scattered *A. xanthogrammica* lower down. In the low intertidal zone and subtidally *Metridium senile* is common, as is *Ascidia ceretodes*. The bryo-

zoans *Celleporaria brunnea* and *Bugula neritina* are common near the low tide line. *Corynactis californica* also occurs at this level in a patchy distribution. The asteroid *Pisaster ochraceus* is abundant in the low intertidal and subtidal area on the sea wall.

The diagonal bracing piles of the sea wall carry dense, heavy populations of organisms similar to those on the piles under the main part of the wharf further seaward. The same plants found on the sea wall are represented on these piles, but, in addition, the low intertidal region supports numbers of red algae including *Gigartina leptorhynchus* J. Agardh, 1885, *Platythamnion villosum* Kylin, 1925, *Gellidium pusillum* (Stackhouse) Le Jolis, 1863, *Polysiphonia pacifica* Hollenberg, 1942, and *Centroceras clavatum* (C. Agardh) Montagne, 1846.

The animals inhabiting the bracing piles are similar to those found on the fender piles along the entire eastern side of the wharf (see below) and in the low intertidal area and subtidally *Balanus nubilus* forms massive collars around each pile. The collars are populated by great numbers of other organisms which will be described later in connection with the piles under the main wharf. Of all the piles associated with the wharf, these sloping piles are unique in often having dense clumps of *Pollicipes polymerus* high up in the intertidal zone, but on the under, somewhat protected, side of the pile.

b. Fauna and Flora of Main Wharf Piles

In later sections of this report we will present in detail our observations on organisms living on a few selected concrete piles under the main wharf. In this section we will merely give an overview of what a casual observer or diver would see in examining piles under the seaward half of Municipal Wharf No. 2.

When we began making observations we suspected we could see some distinct differences between the populations on wooden piles and those on the concrete piles. For example, it appeared that the anemone *Metridium senile* preferred a wood substrate and the anemone *Corynactis californica* preferred concrete. Also, the large masses of the tube worm *Phyllochaetopterus prolifica* were much more common on concrete piles than on wood. When one examines the oldest wooden piles under the wharf, however, piles from which most of the surface creosote has leached out, one finds these piles carry populations similar to those on the concrete (except for masses of *Phyllochaetopterus*). The fouling population on some wooden piles has been altered due to the destructive effect of the gribble *Limnoria quadripunctata* Holthuis, 1949, where the surface of the wood has been weakened to the extent that

large masses of fouling growth become dislodged and fall to the bottom.

On taking a small boat or raft under the wharf at a period of low tide the observer can examine a vast array of sessile invertebrates and algae attached to the piles in the intertidal zone. The cluster of organisms circling the piles gets thicker as one proceeds down each pile to the low water mark and at about the 0.0 m tide level most piles possess a well-defined collar made up of the fouling growth. In some cases this collar extends out from the pile for 0.5 m or more. Clones of small anemones (*Corynactis*) give most of the piles splashes of color in the lower intertidal zone. As one proceeds along a row of piles from the east to the west side of the wharf the most obvious difference one sees in the populations occupying the intertidal region is the dominance of small individuals of the anemone *Metridium senile* throughout the middle and lower part of the zone on the eastern piles, and their nearly complete replacement on the inner piles and to the west by the anemones *Anthopleura elegantissima* and *Corynactis californica*. Macroscopic marine algae, common on the piles both on the east and west side of the wharf, are not found on the innermost piles. On most of the piles, the upper intertidal area is populated by the acorn barnacles *Balanus glandula* and *Chthamalus dalli* down to about 1.0 m above MLLW. Between the +1.0 and +0.5 m level the dominant barnacle is *Tetraclita squamosa rubescens* and below this, forming the basis for the distinct collar around each pile, are clusters of the giant acorn barnacle *Balanus nubilus*, or masses of the tube worms *Phyllochaetopterus prolifica*. Large clusters of the cirratulid worm *Dodecaceria fewkesi* are also found on or adjacent to the acorn barnacles.

As one moves seaward among the rows of piles, the changes in the populations in the intertidal region are more subtle, and it is only on the outermost rows of piles that distinct differences are noted. On these piles, subject to more wave action, organisms extend further up and *Balanus glandula* may be found 2.5 m or more above MLLW. In addition, the lower half of the intertidal zone is dominated by exceedingly large solitary green anemones (*Anthopleura xanthogrammica*), some individuals with crowns 25 cm in diameter. The barnacles *Balanus nubilus* and *B. tintinnabulum* form the basis for the collar around these piles at the end of the wharf.

Subtidally, the piles in any one row again show differences as one moves from east to west, but are more uniform in populations of organisms as one moves seaward along the wharf. As in the intertidal zone, the outer piles on the east are dominated by *Metridium senile*, some large and solitary, attached to the pile nearly all the way to the

bottom, whereas, *Metridium* is uncommon on the inner piles and those to the west.

Each row of piles carries a somewhat different population from any other row, but by comparing the dominant organisms found on a series of piles along the eastern side of the main wharf with a similar series along the western side we can gain a fair idea of the populations on the piles of the wharf as a whole. Except for the marine plants, the innermost piles carry populations somewhere between these extremes. In Figures 5 and 6 we present combined observational data taken from the intertidal area and while diving on 14 wooden and concrete piles from both the east and west sides of the main wharf, and from the examination of 13 wooden fender piles removed from the east side of the wharf and 12 such piles removed from the west side.

In Figures 5 and 6 only the vertical distributions of the dominant sessile organisms are plotted and no attempt is made to quantify the populations. The larger mobile benthic animals living on the piles are not listed, but on many piles these make up a significant amount of the biomass. Throughout the intertidal zone the sea star *Pisaster ochraceus* is abundant. High on the piles the lined shore crab *Pachygrapsus crassipes* Randall, 1839, the limpets *Collisella digitalis* and *C. scabra*, and the littorines *Littorina scutulata* and *L. planaxis* are common. In the low intertidal zone, and particularly subtidally, one commonly finds the asteroids *Patiria miniata*, *Dermasterias imbricata*, *Pisaster brevispinus*, *P. giganteus*, and *Pycnopodia helianthoides* (Brandt, 1835). The large holothurian *Stichopus californicus* (Stimpson, 1857) is occasionally seen subtidally on the piles as are the crabs *Pugettia producta* and *Loxorhynchus crispatus*. In the lower intertidal zone and subtidally among the sessile organisms the opisthobranchs *Hermisenda crassicornis*, *Polycera atra*, *Aeolidia papillosa*, *Acanthodoris brunnea*, *Aegires albopunctatus*, and *Trinchesia albocrusta* are sometimes common.

DETAILED STUDY OF INTERTIDAL ORGANISMS LIVING ON FOUR SELECTED CONCRETE PILES

The above sections of this paper have discussed the general distribution of the largest and most obvious organisms living on the piles under the wharf observed as one grossly examines the piles. In the recesses between and under the larger organisms, however, lives a hoard of smaller organisms, mainly worms and small arthropods. The major effort of this investigation was devoted to a qualitative

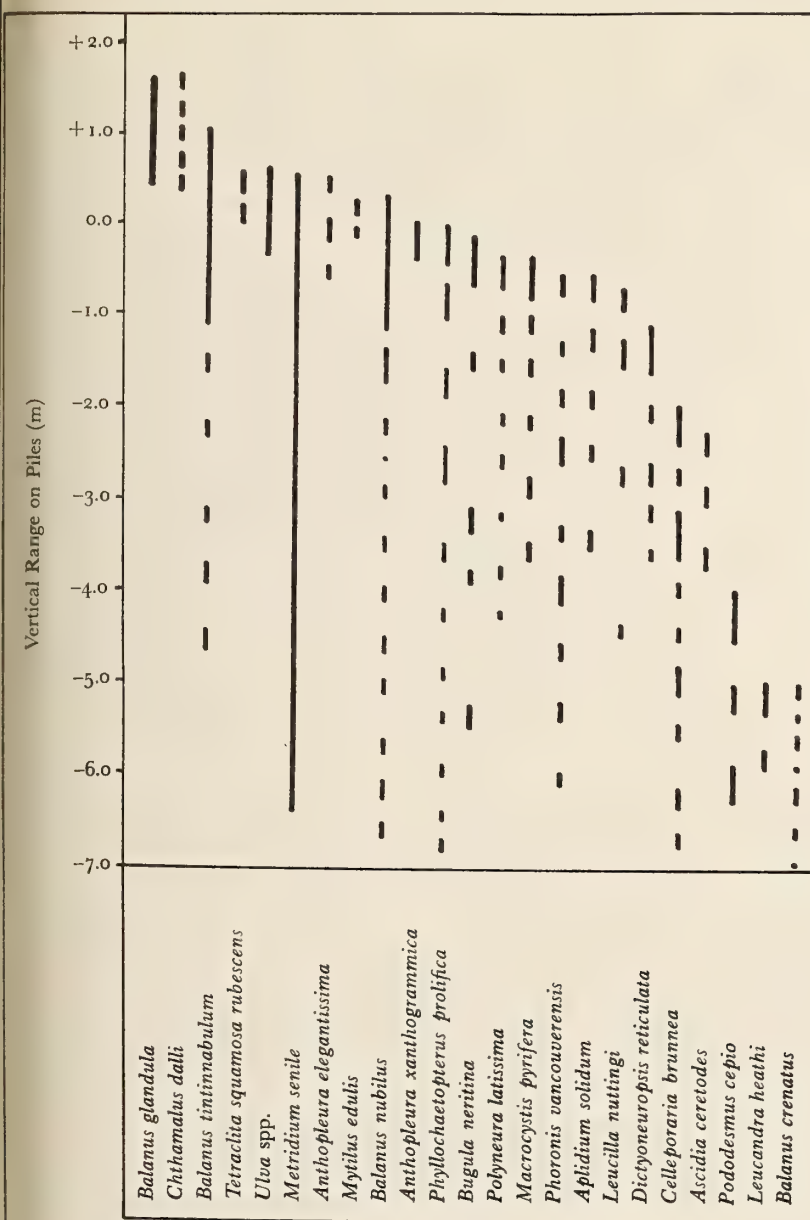


Figure 5

Vertical Distribution of Organisms on Piles on East Side of Wharf

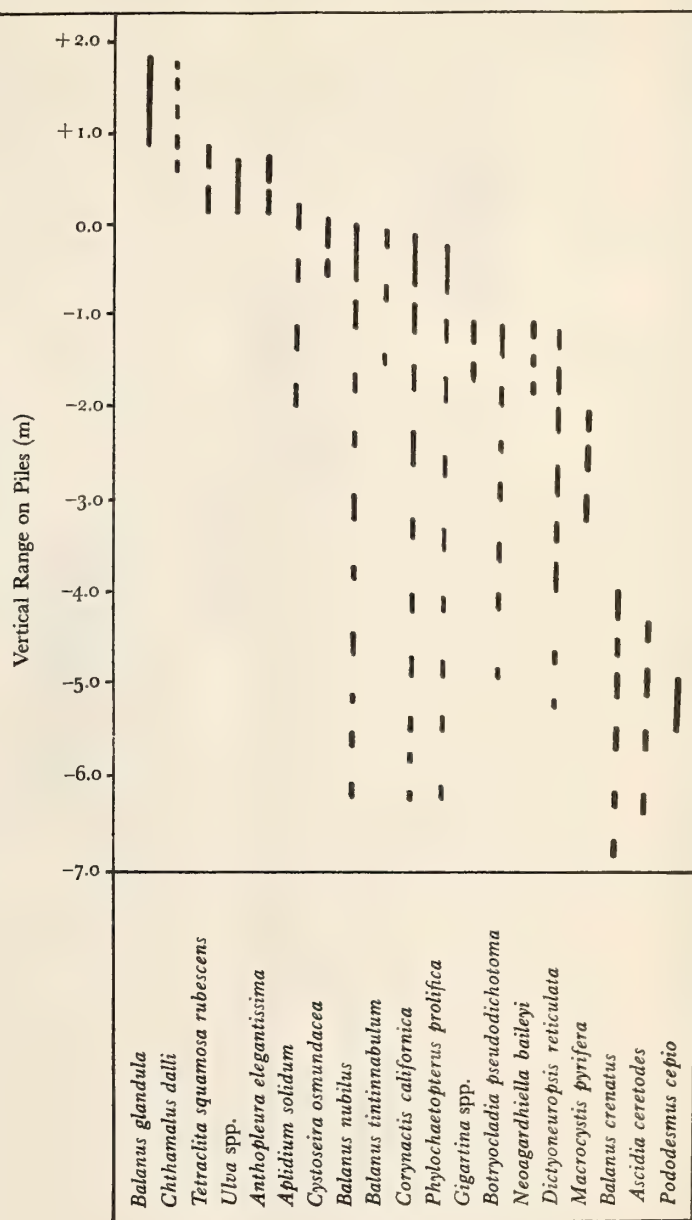


Figure 6

Vertical Distribution of Organisms on Piles on West Side of Wharf

and quantitative analysis of the entire fauna on a few selected concrete piles in a single row under the main wharf (see above and Figure 3). This necessitated scraping the piles down to the substrate to remove all living organisms attached to or moving about on the pile or among the sessile organisms, and then weighing, identifying and counting the macroscopic organisms found on each vertical increment of the pile (see above, Methods).

The organisms living on the intertidal sections of each of the 4 piles were fairly easy to study and collect from a raft at low tide. We have therefore been able to make a detailed comparison of the intertidal fauna occupying these sections on Piles A, B, C and D. Figures 7-10 illustrate the general vertical distribution of the most obvious animals on each of the piles and give a rough measure of their abundance. Data for these figures were

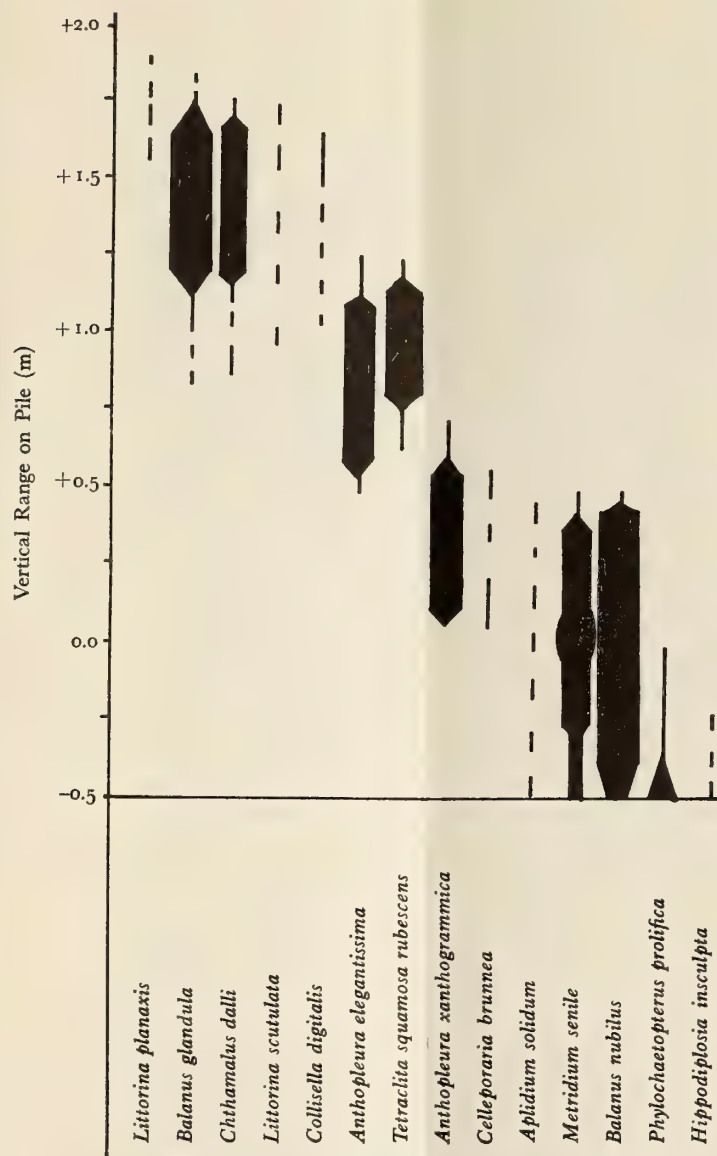


Figure 7

Pile A Vertical Distribution of Animals in the Intertidal Area
The width of the bars indicates relative density of individuals of the species at any one level

collected prior to the removal and analysis of the fouling growth, so only those organisms visible and identifiable in place on the pile were included. Only Piles A and D carried any macroscopic algae in the intertidal zone. These algae were the same as those indicated in Figures 5 and 6 of the general survey and are not shown in Figures 7 and 10 but are discussed below. Table 1 lists in more detail all of the animals and plants identified after scrap-

ing the fouling growth from the intertidal section of each pile.

Although each of the 4 concrete piles studied has many of the same species as part of the fouling growth in the intertidal region, the proportion, distribution, abundance and dominance of each species varies from pile to pile, and some piles totally lack animals that may be dominant on a pile close by. At the present time we know next to nothing about the reasons for these differences. The only physical parameter that is obviously different from pile to pile at the study site is the amount of light available, there being some direct morning sunlight on Pile A, and a greater amount of afternoon sunlight on Pile D. Pile B is part-way and Pile C is mid-way along the row under the wharf and both are subject to dim light conditions most of the time. Yet, as will be seen, even piles with roughly the same light conditions each carry a slightly different mix of fouling organisms. Pile A, being on the exposed eastern side of the wharf, is subject to slightly more wave action than the other piles.

Using the data shown in Figures 7-10 and Table 1, plus additional observations and measurements, the fouling communities on each of the four study piles will be discussed separately. The populations on these piles are perhaps climax communities for they represent ecological succession and replacement over a period of 50 years. During the period the piles have been in place they have not been disturbed seriously in any way.

Pile A (Figure 7)

Pile A is the easternmost concrete pile in the row studied; it is approximately 2 m inward from the outer edge of the wharf. A wooden fender pile 1.5 m to the northeast is at the wharf's edge.

When viewed at low tide Pile A is seen to carry three distinct bands of living animals, each band merging with the next. These will be discussed from top to bottom and the height measurements will be from 0.0 m tide level (MLLW).

+1.8 to +1.2 m. *Balanus glandula* is dominant with the smaller barnacle *Chthamalus dalli* second in abundance. Scattered between the barnacles are isolated limpets (*Collisella digitalis*) and littorines (*Littorina scutulata* and *L. planaxis*).

Balanus glandula individuals are well-separated at the extreme upper limit of the range and are large (average 2 cm basal diameter). At about +1.7 m these barnacles become clustered and the largest are 1 cm or less. In the area of densest concentration (approximately +1.5 to +1.2 m) the barnacles cover the piling surface in concentrations

of 0.8–1.0/cm² depending on individual size. In general *B. glandula* become smaller at lower levels.

Chthamalus dalli begin just below the highest *Balanus glandula* and extend down the pile between individuals of the larger barnacles. Again, the highest barnacles are the largest (0.5 cm diameter) and at +1.5 m average 0.1/cm², but very small individuals in basal contact may exceed 6/cm².

+1.2 to +0.6 m. This band or zone is dominated by the aggregate anemone *Anthopleura elegantissima*, but about equally abundant are thatched barnacles (*Tetracita squamosa rubescens*). When seen from a distance this section of the pile seems solidly covered with anemones which average 5 cm in diameter at the upper end of their range, but when less crowded at the lower levels attain diameters of 10 cm. In spaces between the anemones *Tetracita* are found. The largest of these (3.5 cm diameter) are between the +1.2 and +1.0 m level. Clusters of smaller *Tetracita* occur at +1.0 m in concentrations up to 1/cm². Most of the *Tetracita* on this and other piles are overgrown or covered by a film of unidentified white or gray material that masks the reddish color of the barnacles.

+0.6 to -0.5 m. This low tide zone is dominated by three large organisms: *Balanus nubilus* and *Anthopleura xanthogrammica* dominate the upper part of the zone, *Metridium senile* gradually replaces *Anthopleura* and dominates the lower part of the zone. In addition, this zone supports large colonies of *Celleporaria brunnea*, and at the very lowest part of the zone a thick collar of worm tubes (*Phyllochaetopterus prolifica*) begins and continues subtidally. Attached to the worm tubes are colonies of the ascidian *Aplidium solidum* and the bryozoan *Hippodiplosia insculpta*.

Balanus nubilus averages 10–15 cm in basal diameter in the zone and often pile upon one another to form clusters so that it is impossible to count them *in situ*. They thin out in the lower part of the zone but extend down subtidally as isolated individuals.

Anthopleura xanthogrammica occur as large (10 cm diameter) isolated individuals between the giant barnacles, and because of individual size contribute significantly to the biomass of the zone.

Metridium senile are small (3 cm diameter) throughout most of the intertidal range, and at about the 0.0 m level they are dominant, circling the pile in dense clusters with individuals in contact. Subtidally on Pile A solitary *Metridium* attain large size (>15 cm diameter, see below).

In addition to the animals discussed above, Pile A is colonized in the intertidal zone on the eastern side by the

green alga *Ulva* spp. from the +1.0 to the +0.3 m level. The plant attaches either to bare patches of the concrete or to barnacles. Each plant is usually small (<5 cm long). In addition the following red algae are found on the pile in the low intertidal zone: *Rhodomenia pacifica*, *Polysiphonia latissima*, and *Pterosiphonia dendroidea*. None of these plants contributes significantly to the total biomass. The brown alga *Dictyoneuropsis reticulata*, is represented by 2 large plants near the -0.5 m level.

Pile B (Figure 8)

This pile is 4 m to the west of Pile A and is under the wharf far enough to be in dim light most of the day. In many respects it carries a fouling growth that is more typical of the concrete piles under the wharf than any of the others reported on here. Like the majority of the 360 concrete piles under the main wharf it has an extensive collar of fouling growth either partially or completely ringing the pile in the lowest intertidal zone. This collar is composed primarily of *Balanus nubilus* clustered and piled on top of one another forming a mass extending out 0.5 m or more from the surface of the pile. Most of the barnacles forming the foundation of the collar are dead, having long since been smothered by those growing on top of them, but these long-dead shells are so securely cemented to the pile that one must remove them with hammer and chisel except where they have been weakened by extensive penetration by the boring sponge *Cliona celata*. The *Balanus nubilus* collar is practically covered by dense colonies of *Corynactis californica*.

This pile also has three obvious bands of animals in the intertidal zone, although the middle zone is relatively sparsely populated.

+1.75 to +0.75 m. This band 1 m in vertical extent is dominated by acorn barnacles; *Balanus glandula* and *Chthamalus dalli* extend from +1.75 m down to +1.0 m where they rapidly taper off and are replaced by *Tetracita squamosa rubescens*.

Balanus glandula are few and scattered at the upper extent of their range and average 1 cm in diameter. At just below the 1.5 m level they become very dense and average 0.7 cm in diameter and are in basal contact practically covering the pile.

Chthamalus dalli occupies roughly the same range as *Balanus glandula* but becomes abundant at the 1.7 m level where animals of 0.5 cm basal diameter occur in concentrations of 1/cm².

Tetracita occurs as isolated individuals at and just below the +1.25 m level, but becomes abundant only at +1.0 m where the other two barnacles gradually disappear. The upper individuals are largest (3 cm); those at the

Species living on four concrete piles in Monterey Harbor.

[illegible]

Table 1 (continued)

Species List	Max. Size mm	Pile A										Pile B		Pile C		Pile D				
		+2.0 to +1.5m	+1.5 to +1.0m	+1.0 to +0.5m	+0.5 to 0.0m	0.0 to -0.5m	-0.5 to -1.0m	-1.0 to -1.5m	-1.5 to -2.0m	-2.0 to -2.5m	-2.5 to -3.0m	-3.0 to -3.5m	-3.5 to -4.0m	-4.0 to -4.5m	-4.5 to -5.0m	-5.0 to -5.5m	-5.5 to -6.0m	-6.0 to -6.5m	-6.5 to -7.0m	-7.0 to -7.5m
<i>Lineus vegetus</i> Coe, 1931	40					R	R												R	
<i>Micrura pardalis</i> Coe, 1905	20					R											R			
<i>Micrura verrilli</i> Coe, 1901	70					O	O	R			R									
<i>Amphiporus bimaculatus</i> Coe, 1901	60					A	F	O	O											R
<i>Amphiporus imparispinosus</i> Griffin, 1898	15					O	O	R		R									R	
<i>Emplectonema gracile</i> (Johnston, 1837)	150	O	A	O	O													O		R
<i>Nemertopsis gracilis</i> Coe, 1904	100	R																		
<i>Paranemerites peregrina</i> Coe, 1901	30		R					R												
<i>Tetrastemma nigrifrons</i> Coe, 1904	40							R	O						R					
Sipuncula																				
<i>Phascolosoma agassizii</i> Keferstein, 1867	120		F	F	F	A	A	O	O	O	F		O	O	F	O	O	O		
Annelida																				
<i>Eunoe barbata</i> Moore, 1910	20					R														
<i>Halosydna brevisetosa</i> Kinberg, 1855	100		O	F	A	A	A	A	A	F	F	F	A	A	F	A	O		O	A
<i>Halosydna tuberculifera</i> Chamberlain, 1919	80																		O	R
<i>Lepidonotus squamatus</i> (Linnaeus, 1767)	5					R														
<i>Thormora johnstoni</i> (Kinberg, 1855)	15					R				R										
<i>Peisidice aspera</i> Johnson, 1897	15				F	A	A	F	A	F	F	O	F	O	F	F	O	O		
<i>Paleonotus bellis</i> (Johnson, 1897)	20										R	O	R	R	R	R	O	R		
<i>Anatides groenlandica</i> (Oersted, 1843)	50						R	R												
<i>Anatides madeirensis</i> (Langerhans, 1880)	35						R	O	R									R		
<i>Anatides mucosa</i> (Oersted, 1843)	15						R													
<i>Anatides williamsi</i> Hartman, 1936	25													R	R	R				
<i>Eleone californica</i> Hartman, 1936	10															R	R			
<i>Eulalia aviculiseta</i> Hartman, 1936	30				R	A	A	A	F	A		F	A	O	O	F	F	O		R
<i>Eulalia bilineata</i> (Johnston, 1840)	40					O	O	F	R				O	O	O	R				
<i>Eulalia viridis</i> (Linnaeus, 1767)	60					R							R							
<i>Eumidia bifoliata</i> (Moore, 1909)	20				O	A	A	A	O	R		R						R		
<i>Genetyllis castanea</i> (Marenzeller, 1879)	15					F	O	O										R		
<i>Notophyllum imbricatum</i> Moore, 1906	100							R												
<i>Sige californiensis</i> Chamberlin, 1919	15						R	R		R										
<i>Amphiduros pacificus</i> Hartman, 1961	20					F	O	O	R	R			R							
<i>Ophiodromus pugettensis</i> (Johnson, 1901)	30				O	A	A	F	F	O	R	O	R	F		O			O	
<i>Amblosyllis</i> sp.	15					O	O		R	R										
<i>Autolytus varius</i> Treadwell, 1914	30											R				R				
<i>Eusyllis assimilis</i> Marenzeller, 1875	15									R										
<i>Exogone</i> sp.	5							R												
<i>Haplosyllis spongicola</i> (Grube, 1855)	40					F	F	A	F		R	O				R				
<i>Odontosyllis phosphorea</i> Moore, 1909	30					F	A	O	O	R								O	F	
<i>Odontosyllis</i> sp.	20					F	A	F	O										F	
<i>Pionosyllis gigantea</i> Moore, 1908	15							R												
<i>Syllis elongata</i> (Johnson, 1901)	35				A	A	O	R	O	O	F		O	R	F	R	O	O		F
<i>Syllis gracilis</i> Grube, 1840	30		O	O		A	A	O	O	O	O	F	F	R		R	O	O		
<i>Typosyllis aciculata</i> Treadwell, 1945	10					F	R		O	R										
<i>Typosyllis adamanteus</i> (Treadwell, 1914)	10																			
<i>Typosyllis bella</i> Chamberlin, 1919	20							R												
<i>Typosyllis fasciata</i> Malmgren, 1867	20					O	O		R	R		O						O		
<i>Typosyllis hyalina</i> (Grube, 1863)	20					F	A	A	O	O	F						R	R		
<i>Typosyllis pulchra</i> Berkeley & Berkeley, 1938	20						R				O									

			Pile A										Pile B			Pile C			Pile D																
			+2.0 to +1.5m	+1.5 to +1.0m	+1.0 to +0.5m	0.0 to -0.5m	-0.5 to -1.0m	-1.0 to -1.5m	-1.5 to -2.0m	-2.0 to -2.5m	-2.5 to -3.0m	-3.0 to -3.5m	-3.5 to -4.0m	-4.0 to -4.5m	-4.5 to -5.0m	-5.0 to -5.5m	-5.5 to -6.0m	-6.0 to -6.5m	-6.5 to -7.0m		+2.0 to +1.5m	+1.5 to +1.0m	+1.0 to +0.5m	+0.5 to 0.0m	0.0 to -0.5m	+1.5 to +1.0m	+1.0 to +0.5m	+0.5 to 0.0m	+2.0 to +1.5m	+1.5 to +1.0m	+1.0 to +0.5m	+0.5 to 0.0m			
		Pile Increment →																																	
		Species List ↓	Max Size mm																																
		<i>Neanthes caudata</i> (delle Chiaje, 1828)	30				O																												
		<i>Nereis eakini</i> Hartman, 1936	100			F	A	A	F	O	R	R	O	R	O	O	O					R	F			F							F		
		<i>Nereis latescens</i> Chamberlin, 1919	40				O		R	R	R																								
		<i>Nereis natans</i> Hartman, 1936	15				R		O						R																				O
		<i>Nereis grubei</i> (Kinberg, 1866)	15				O																												
		<i>Nereis pelagica neonigripes</i> Hartman, 1936	30	R	R	R	R															R	O		R										
		<i>Nereis vexillosa</i> Grube, 1851	20											R																			R	R	
		<i>Nereis zonata</i> Malmgren, 1867	60				O	R	F						R					R															
		<i>Platynereis bicanaliculata</i> (Baird, 1863)	70			F	A	F	F		R		O			O																		F	
		<i>Pseudonereis</i> , sp.	20					R			R	R																							
		<i>Palola paloloides</i> (Moore, 1909)	200						R	O	R	R	R																						
		<i>Dorvillea moniloceras</i> (Moore, 1909)	60			F	A	A	A	F	O	F	F	O	F	O	O	O	F			F	A			F	F	F					F	A	
		<i>Dorvillea rudolphii</i> Hartman, 1938	25				O	R	R																										
		<i>Lumbrineris erecta</i> (Moore, 1904)	220			F	A	A	F	F	F	O	F	A	F	F	O	O																F	R
		<i>Lumbrineris tetraura</i> (Schmarda, 1861)	100	R	R		R						R	R	R	O	R						O												
		<i>Lumbrineris zonata</i> (Johnson, 1911)	30				O		R						R																				
		<i>Limbrineris bicirrata</i> Treadwell, 1929	50																								O								
		<i>Arabella tricolor</i> (Montagu, 1804)	300				A	A	F						O	R	O	O	O														O	A	
		<i>Arabella semimaculata</i> (Moore, 1911)	100	O	O																														

			Pile A										Pile B			Pile C			Pile D																
			+2.0 to +1.5m	+1.5 to +1.0m	+1.0 to +0.5m	+0.5 to 0.0m	0.0 to -0.5m	-0.5 to -1.0m	-1.0 to -1.5m	-1.5 to -2.0m	-2.0 to -2.5m	-2.5 to -3.0m	-3.0 to -3.5m	-3.5 to -4.0m	-4.0 to -4.5m	-4.5 to -5.0m	-5.0 to -5.5m	-5.5 to -6.0m	-6.0 to -6.5m	-6.5 to -7.0m	+2.0 to +1.5m	+1.5 to +1.0m	+1.0 to +0.5m	+0.5 to 0.0m	0.0 to -0.5m	+2.0 to +1.5m	+1.5 to +1.0m	+1.0 to +0.5m	+0.5 to 0.0m	0.0 to -0.5m					
Pile Increment →	Species List ↓	Max. Size mm																																	
	<i>Serpula vermicularis</i> Linnaeus, 1767	100				O	O	F	O	F	O	F	O	R	O	O	R	O	R	A				R						R		O			
	<i>Spirorbis borealis</i> Daudin, 1800	5				A	A	A	A	A	A	A	A	A	A	A	A	A	A	A			O												
	<i>Spirorbis eximius</i> Bush, 1904	5				A	A	A	A	A	A	A	A	A	A	A	A	A	A	A			O												
	<i>Spirorbis moerchi</i> Levinsen, 1883	5				A	A	A	A	A	A	A	A	A	A	A	A	A	A	A			O												
	<i>Spirorbis spirillum</i> (Linnaeus, 1758)	5				O	A	A	A	A	A	A	A	A	A	A	A	A	A	A			O	O											
	<i>Spirorbis</i> spp.	5				A	A	A	A	A	A	A	A	A	A	A	A	A	A	A			O												
Arthropoda																																			
	<i>Balanus glandula</i> , Darwin 1854	20	A	A	O																	F	A	R			A	A	O		O	R			
	<i>Balanus aquila</i> Pilsbry, 1907	50																	R																
	<i>Balanus crenatus</i> Bruguière, 1897	10				A	A	A	A	F	F	O	A	O	F	A	A	A	A	A						F						O	R		
	<i>Balanus nubilus</i> Darwin, 1854	150				A	F	R	R	O	R	O	O	O	R	F	R	O	O	O						R	A			O	F		O	R	
	<i>Balanus tintinnabulum</i> Pilsbry, 1916	40				R	R	R		R						R									R	R	O		R	R	R		O	R	
	<i>Chthamalus dalli</i> Pilsbry, 1916	5	F	F	O																	A	A	O			A	A	O		A	O	R		
	<i>Tetractia squamosa rubescens</i> Darwin, 1854	50			A	A																	F	A	F		A	A	F		A	A	R		
	<i>Pollicipes polymeris</i> Sowerby, 1833	40																								R									
	<i>Idotea resicata</i> Stimpson, 1857	20						R	O	R	R																						R		
	<i>Jaeropsis dubia dubia</i> Menzies, 1951	10						A	A	O	F																								
	<i>Accedomoera vagar</i> Barnard, 1969	7						R																											
	<i>Atylus levidensus</i> Barnard, 1956	10						R																											
	<i>Corophium insidiosum</i> Crawford, 1937	5						A	A	A	A	A	O		A	O	A	F	F	A															
	<i>Micropotopus</i> sp.	10									R																								
	<i>Perotripus brevis</i> (LaFollette, 1915)	5						A	A	A	A	A	F	A	A	A	A	F	A							F	A					A	O		
	<i>Deutella californica</i> Mayer, 1890	5						A	A	A		R					R									F	A						A	O	
	<i>Tritella laevis</i> Mayer, 1903	5						A	A	A	A	A	O	A	A	A	A	F	F							A							A	A	
	<i>Caprella verrucosa</i> Boeck, 1871	10						R																											
	<i>Heptacarpus paludicola</i> Holmes, 1900	30						F	O																										
	<i>Heptacarpus taylori</i> (Stimpson, 1857)	20						R	R										R																
	<i>Spirontocaris prionota</i> (Stimpson, 1854)	30																	R																
	<i>Alpheus dentipes</i> Guérin, 1832	20																		R													R	O	
	<i>Bateus harfordi</i> (Kingsley, 1878)	50													R												R								
	<i>Loxorhynchus crispatus</i> Stimpson, 1857	150						O				R				R																			
	<i>Mimulus foliatus</i> Stimpson, 1860	20						R																										A	R
	<i>Pugettia producta</i> (Randall, 1839)	40						R		R				R													R							R	R
	<i>Cancer antennarius</i> Stimpson, 1856	70				R	O	A	F	R		R		R		R	R									R									
	<i>Cancer jordani</i> Rathbun, 1900	30						R	F	A																									
	<i>Cancer</i> sp.	20						F	F		F	R																							
	<i>Lophopanepeus bellus</i> (Stimpson, 1860)	25						R	F	F	O			R	R		R	R									R							O	
	<i>Pinnixa longipes</i> (Lockington, 1877)	12						R																											
	<i>Pachycheles pubescens</i> Holmes, 1900	20															R			R															
	<i>Pachycheles rudis</i> Stimpson, 1859	20						R	A								R																		
	<i>Paraxanthias taylori</i> (Stimpson, 1860)	10																																	
	<i>Petrolisthes cinctipes</i> (Randall, 1839)	15								R																									
	<i>Phoxichilidium femoratum</i> (Rathke, 1799)	10						R																											
	<i>Pycnogonum stearnsi</i> Ives, 1892	10				F		A	A	A	A	R	R	R		R	R		R	R	R														
Mollusca																																			
	<i>Callistochiton crassicosatus</i> Pilsbry, 1893	30																																	
	<i>Lepidozona californiensis</i> Berry, 1931	20						R	A	F				R	R																				
	<i>Lepidozona mertensii</i> (Middendorff, 1846)	20								R																									
	<i>Mopalia ciliata</i> (Sowerby, 1840)	40												R						R															

[illegible]

[illegible]

Table 1 (continued)

Species List ↓	Max. Size mm	Pile A										Pile B		Pile C		Pile D				
		+2.0 to +1.5m	+1.5 to +1.0m	+1.0 to +0.5m	+0.5 to 0.0m	0.0 to -0.5m	-0.5 to -1.0m	-1.0 to -1.5m	-1.5 to -2.0m	-2.0 to -2.5m	-2.5 to -3.0m	-3.0 to -3.5m	-3.5 to -4.0m	-4.0 to -4.5m	-4.5 to -5.0m	-5.0 to -5.5m	-5.5 to -6.0m	-6.0 to -6.5m	-6.5 to -7.0m	+7.0 to +7.5m
<i>Eupentacta quinquesemita</i> (Selenka, 1867)	10				O	R														A
<i>Cucumberia miniata</i> Brandt, 1835	50																			O
Chordata (Urochordata)																				
<i>Aplidium solidum</i> (Ritter & Forsyth, 1917)	170	P	P	P	P	F	A	O	R	F	F	F	R	R	F	F	O	R		
<i>Ascidia ceretodes</i> (Huntsman, 1912)	30				O	O	R	O	R	R	O	F	O	O	O	O	O	R		
<i>Pyura haustor</i> (Stimpson, 1864)	15																			R
<i>Styela montereyensis</i> (Dall, 1872)	40				O	R	R													F
<i>Styela truncata</i> Ritter, 1901	10	R	R	R	R	R														R
Wet Weight of Fouling Growth (Biomass) Removed from Pile (kg)		0.15	0.63	17.91	16.23	22.22	11.58	6.81	4.99	4.77	6.99	8.63	7.58	3.75	10.78	5.83	5.44	3.55	2.92	0.10

Explanation of Table 1

¹ These species are found burrowing into the wall plates of *Balanus nubilus* or the upper valves of *Pododesmus cepio*, or both. Letters in columns refer to relative abundance of individuals of each species at the particular tidal level on 0.5 m² of pile surface:

- R = Rare, 1-5/0.5 m²
 O = Occasional, 6-10/0.5 m²
 F = Frequent, 10-20/0.5 m²
 A = Abundant, 20+/0.5 m²
 P = Present but numbers undetermined (used primarily for colonial animals)

+1.0 m level are 2-3 cm in diameter and often are piled on top of one another giving a density of up to 10 large barnacles in every 100 cm² surface area.

+0.75 to 0.0 m. This middle band on the pile is populated above by scattered *Anthopleura elegantissima* averaging 5 cm in diameter and below by *Anthopleura xanthogrammica*. A few barnacles (*Tetraclita*) extend down to about the +0.25 m level. Encrusting bryozoans (*Celleporaria brunnea*) occur between the anemones and barnacles along with extensive growths of the fuzzy bryozoan *Bowerbankia gracilis*.

0.0 to -0.5 m. This extensive band in the lower part of the intertidal zone is populated by a dense aggregation of animals. *Anthopleura xanthogrammica* average 10 cm

in diameter and are scattered in the upper part of this zone, but the majority of the fouling mass is composed of *Balanus nubilus* covered with *Corynactis californica*. The barnacles are as much as 15 cm in basal diameter and in one area are piled up in layers 8-10 deep, the mass extending out from the pile as a ledge 50 cm and more in width. The outer periphery of the barnacle clusters are often completely covered with clones of *Corynactis californica*, each clone being of somewhat different color ranging from purple to orange to brilliant crimson. These vivid bands of color can be seen in this zone on most of the concrete piles under the wharf. The anemones average 2 cm in diameter and are in basal contact. The barnacle shells make up most of the biomass of this zone. When a large cluster of *Balanus nubilus* is removed from the pile, the innermost dead shells clearly show that these old barnacles, when alive, grew over and smothered many *Tetraclita squamosa rubescens*. Thus, on a newly placed concrete pile, *Tetraclita* apparently settle far down the pile to below the 0.0 m tide level, but are later overgrown by *Balanus nubilus*. The collar becomes somewhat less extensive below the -0.25 m level and is gradually replaced by a heavy growth of tube worms (*Phyllochaetopterus prolifica*) with attached slabs of the colonial ascidian *Aplidium solidum* and numerous colonies of the bryozoan *Hippodiplosia insculpta*.

As can be seen from Table 1, numerous other smaller animals inhabit the spaces between barnacles in the collar. The biomass of this section of Pile B exceeds that found on any other pile studied.

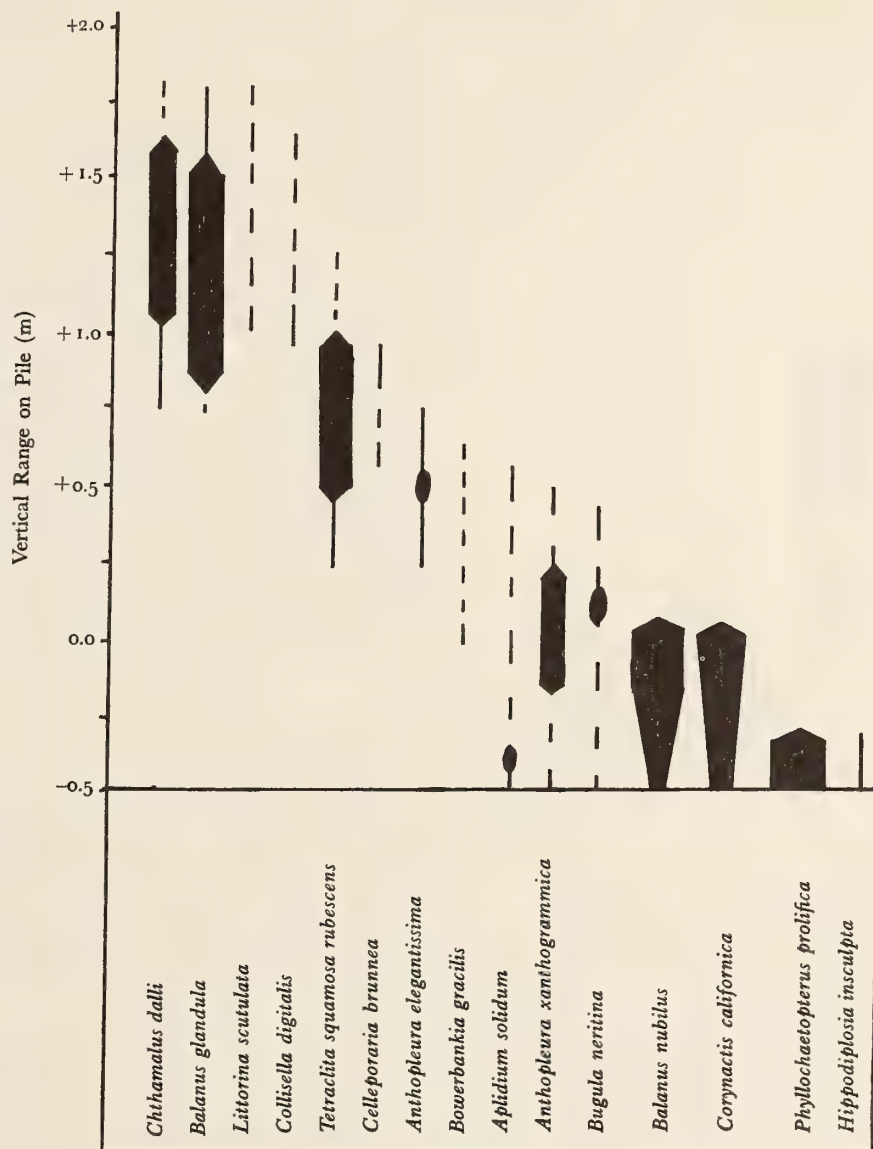


Figure 8

Pile B Vertical Distribution of Animals in the Intertidal Area

The width of the bars indicates relative density of individuals of the species at any one level

Pile C (Figure 9)

Pile C is about midway under the wharf (8 m to the west of Pile B) and has dimmer light conditions than any of the piles being considered here. When seen at low tide Pile C is encircled by 4 rather distinct bands of fouling animals.

+1.75 to +1.0 m. *Balanus glandula* dominates this band. The large solitary individuals first occur at +1.75 and average 2.0 cm in diameter. Between +1.5 and +1.25 m the barnacles average 1 cm in diameter and are in basal contact over most of the surface. Between and on these barnacles, the smaller *Chthamalus dalli* are found in sizes from 0.4 to 0.5 cm and in concentrations up to 4/cm².

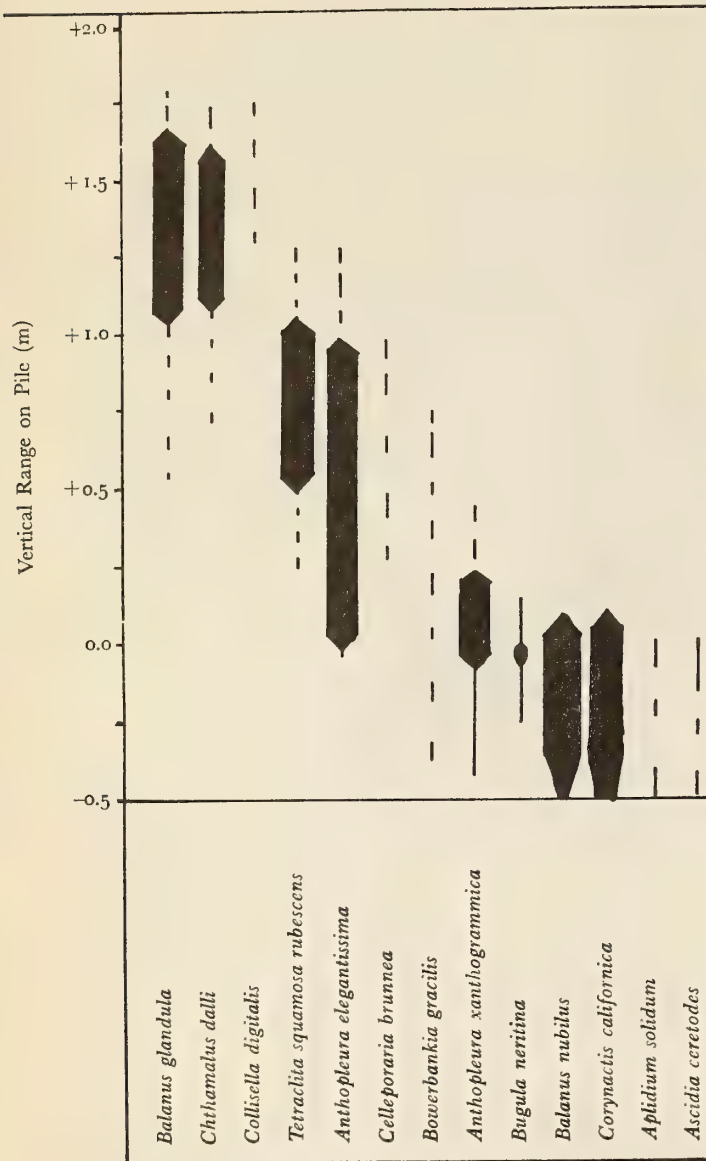


Figure 9

Pile C Vertical Distribution of Animals in the Intertidal Area
The width of the bars indicates relative density of individuals of the species at any one level

+1.0 to +0.5 m. This band is made up primarily of *Tetracita squamosa rubescens* and *Anthopleura elegantissima*. The barnacles are up to 5.0 cm in diameter and in some areas are in basal contact with each other. The anemones scattered between the barnacles average 5 cm in diameter. This band also has an extensive population of

the bryozoans *Celleporaria brunnea* and *Bowerbankia gracilis*.

+0.5 to 0.0 m. *Anthopleura elegantissima* dominates this band and individuals up to 10 cm in diameter are often in basal contact. Scattered among these anemones are a few individual *A. xanthogrammica* up to 15 cm across. In the lowest part of this zone solitary *Balanus nubilus* are found between the anemones.

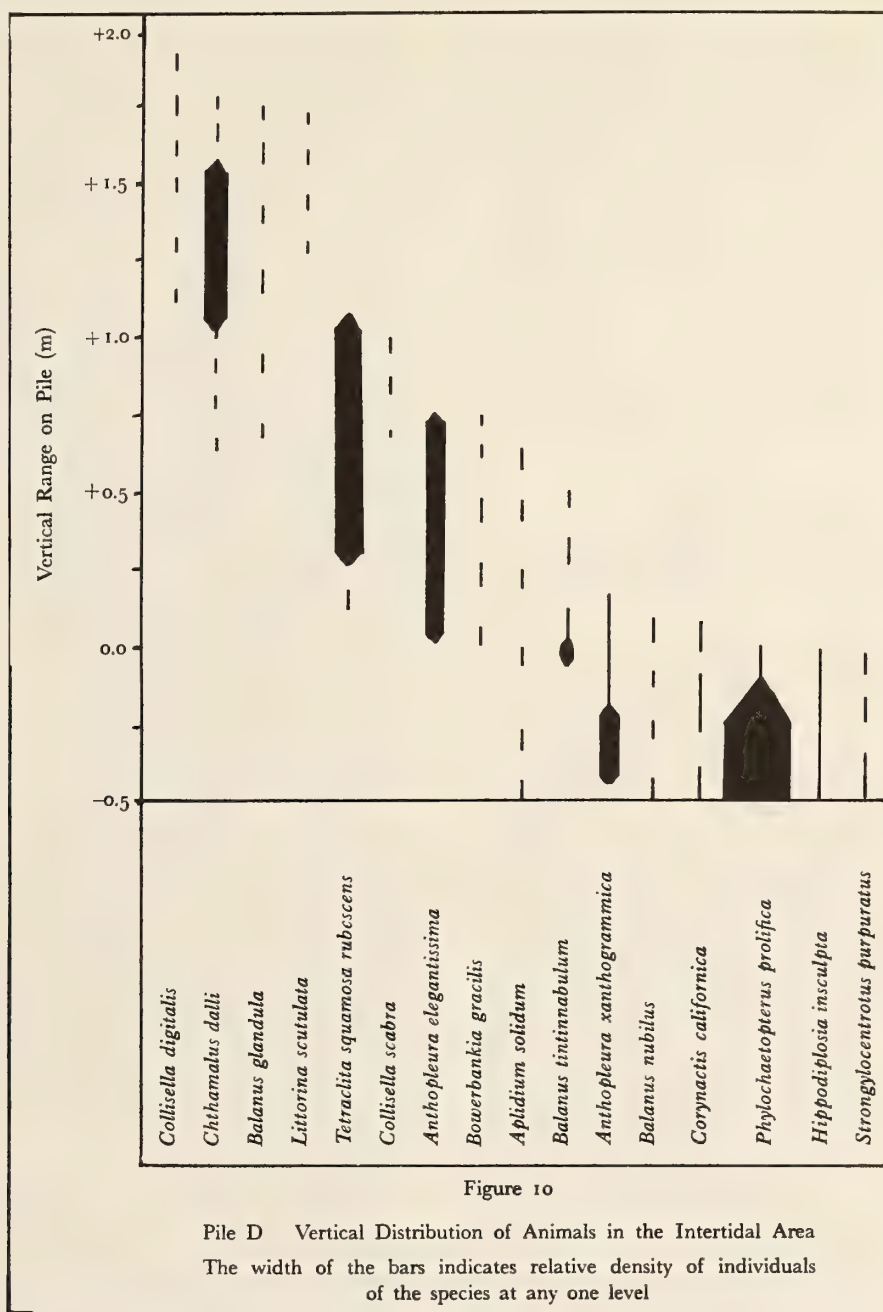
0.0 to -0.5 m. This zone is dominated by *Balanus nubilus*, up to 14 cm in diameter and often in basal contact but not piled up to form a collar. The barnacles are covered with *Corynactis californica* that also spread to cover extensive patches on the concrete piles where the barnacle does not occur. This is the only pile in the series studied that has an extensive population of *Corynactis* directly on the concrete pile surface. Also found in the zone are a few *Anthopleura elegantissima* and a greater number of *A. xanthogrammica* up to 12 cm in diameter. Scattered through the zone are the bryozoans *Bugula neritina* and *Bowerbankia gracilis* and the ascidian *Aplidium solidum* and *Ascidia ceretodes*.

Pile D (Figure 10)

Pile D is the second concrete pile inward from the western end of the row investigated. It is subject to considerable direct sunlight in the late afternoon. The terminal concrete pile just to the west of Pile D is even more exposed to light and has several species of marine algae including *Macrocystis pyrifera* attached to it. Apart from a few small red algae the only visible plants growing in the intertidal zone of Pile D are a few specimens of the brown alga *Dictyoneuropsis reticulata*.

The animal population making up the fouling growth shows quite different distribution and dominance compared to that on the other piles studied, and the animals living on Pile D are fairly typical of those on other concrete piles in other rows along the west side of the wharf. Three major bands of fouling growth can be distinguished.

+1.7 to +1.0 m. In contrast to other piles, this band on Pile D is dominated by *Chthamalus dalli*. The largest of these barnacles average 0.5 cm in diameter, but at high densities (4–5/cm² at +1.0 m) they are somewhat smaller. Scattered through the *Chthamalus dalli* population are a few *Balanus glandula* averaging 1 cm in basal diameter but these are never very abundant. A few limpets (*Collisella digitalis*) and littorines (*Littorina scutulata*) are also found throughout the upper part of this zone and extending above it to approximately the +1.8 m level.



+1.0 to 0.0 m. This second band on Pile D is dominated by *Tetracita squamosa rubescens*. These barnacles are up to 3 cm in diameter at the upper part of their range where they are scattered and isolated. Throughout the middle part of their range they average 2.0 cm in diameter and have an average density of 0.2/cm²; in restricted areas at the +0.5 m level, however, they are clustered with all of their bases in contact. The only other

animal contributing significantly to the biomass in this band is *Anthopleura elegantissima*. Fifteen small specimens averaging 4 cm in diameter are found in the zone. *Bowerbankia gracilis* is found growing over most of the barnacles and on the bare patches of concrete.

0.0 to -0.5 m. This lowest intertidal band on Pile D is dominated by a massive growth of *Phyllochaetopterus prolifica*, the densely clustered and twisted tubes of which

extend outward from the pile for 20 cm or more. Embedded in this tube mass large solitary *Balanus nubilus* are found attached to the pile, each carrying a cluster of *Corynactis californica*. Growing directly on the *Phyllochaetopterus* tubes are massive colonies of the bryozoans *Hippodiplosia insculpta* and *Celleporaria brunnea* and the ascidian *Aplidium solidum*. In spaces between the tubes dozens of purple sea urchins (*Strongylocentrotus purpuratus*) up to 5 cm in diameter are found, and down deep among the worm tubes is a vast assortment of sponges, nemerteans, sipunculids, annelids, mollusks, and small arthropods. It proved impossible to collect and identify all of these, but Table 1 lists the largest and most abundant species.

DETAILED STUDY OF SUBTIDAL ORGANISMS LIVING ON ONE SELECTED CONCRETE PILE

Table 1 presents the list of organisms living on the subtidal portion of the south face of Pile A and includes 235 species of animals and 7 species of plants. As shown by the histogram in Figure 11 there is a definite trend of increasing numbers of species present at the shallower depths. The largest number occurs between -0.5 and -1.5 m in association with the tubed annelid *Phyllochaetopterus prolifica*, the colonies of which along with the barnacle *Balanus nubilus* form a thick collar on the pile between the low intertidal zone and -1.5 m. At its thickest point, this collar extends out 0.4 m from the pile surface.

There is relatively little change in the numbers of species between -2.5 m and -6.0 m. It is in this intermediate range where extensive colonies of *Phoronis vancouverensis* cover a large area of the pile surface. The dense, intertwined tubes of these filter feeders allow very little circulation of water down into their colonies. When scraped from the pile, clouds of black, sulfur-reduced organic material were released into the water from underneath the colonies. The small annelid *Caulleriella alata* is particularly abundant among the *Phoronis* tubes.

Over the deepest half-meter of Pile A bare areas of the concrete surface are exposed. This is believed to be due primarily to the scouring of the pile by the fine-grain bottom sands which are moved by tidal currents. The minute, calcareous tubes of *Spirorbis* spp. and the barnacle *Balanus crenatus* however, are numerous on these areas. Near the bottom, *Metridium senile*, so prevalent at all other depths, is relatively scarce.

On the last dive following collection of organisms from Pile A a general comparison was attempted between this

pile and the others in the same transverse row, primarily Piles B, C and D. The most obvious difference between the populations of subtidal organisms on the four piles is that very few *Metridium senile* are seen on any pile in the row studied other than Pile A. When present on the other piles *Metridium* occur as isolated individuals and are usually much larger, some attaining a crown diameter of 10 cm. The presence of *Corynactis californica* almost reciprocates that of *Metridium* in that none are found on Pile A but they are extremely plentiful on the other piles. While plentiful, their distribution is patchy. This is probably due to the clonal nature of *Corynactis*. Various shades of red, purple and orange delineate different clones that live in close proximity. The abundance of *Corynactis* is inversely proportional to depth, maximum numbers are found in the low intertidal zone. *Anthopleura xanthogrammica* is also seen occasionally in shallow subtidal depths on most of the piles in the row.

Phyllochaetopterus prolifica is much more prevalent at all depths below the collar on Piles B, C, and D than on Pile A. This is particularly true on Pile D where large tube masses are obvious from the low intertidal zone to the bottom. Among these tubes, several large and conspicuous animals are fairly common, including the feather duster worm *Eudistylia* sp. and the holothurians *Eupentacta quinquesemita* and *Cucumaria miniata* (Brandt, 1835). These sea cucumbers are usually completely concealed by the *Phyllochaetopterus* tubes except for their exposed oral tentacles. Another larger holothurian, *Stichopus californicus*, crawls about fully exposed among the worm tubes and the barnacles.

There is little difference in the subtidal *Balanus nubilus* populations on the 4 piles. The tunicates are not as well represented on Piles B, C and D by *Aplidium solidum* as on Pile A either in numbers of colonies or colony size; however, *Ascidia ceratodes* and *Styela montereyensis* are more abundant.

From data contained in Table 1 we have prepared a histogram that compares the number of species found at various depths on Pile A (Figure 11). This histogram also records the total biomass for each 0.5 m² increment. It is clear from this figure that the greatest number of species is found on the pile just at, and immediately below, the lowest tide level (171 species). Most of these organisms are small and are associated with the colonies of *Phyllochaetopterus* on this pile. The greatest biomass, on the other hand, is found between the +1.0 m and 0.0 m tide level. This is the zone populated with the large anemones and the heavy barnacles (*Anthopleura xanthogrammica* and *Balanus nubilus*).

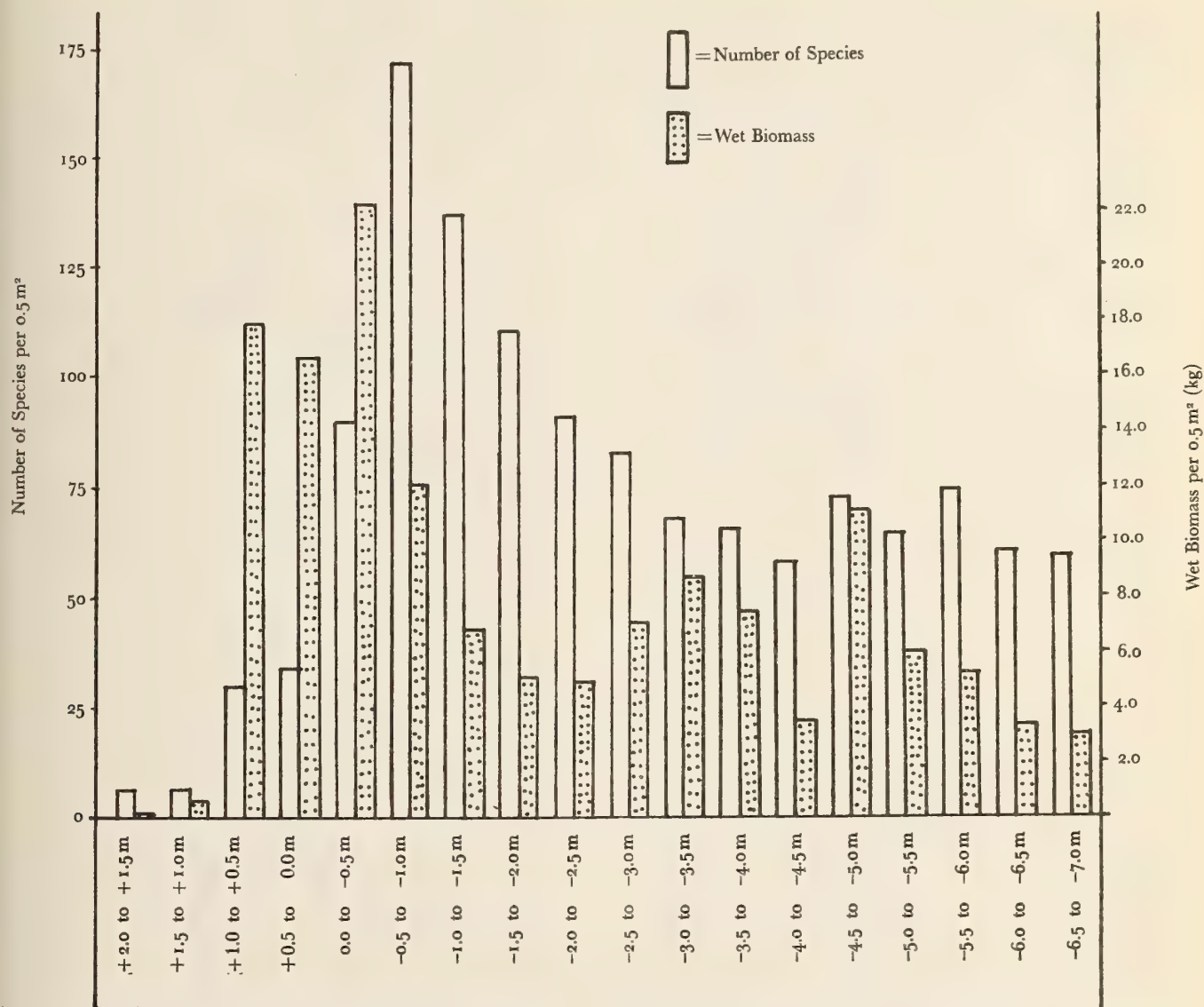


Figure 11

Number of Species and Wet Biomass on 0.5 m Vertical Increments of Pile A

Borers

The wooden piles used for support, bracing, and fenders as part of Municipal Wharf No. 2, as well as the timbers of the sea walls, are pressure-creosoted Douglas fir. This treatment gives temporary protection from marine wood borers depending upon how completely the wood is impregnated with creosote. Some of the wooden piles

remain serviceable for 25 years or more, but others, particularly some of the fender piles subject to wear and abrasion, must be replaced after 5 or 6 years. The timbers of the sea walls, after being in place for 17 years, are now beginning to fail as a result of borer attack.

The most obvious and rapid damage to the wood occurs in the lower intertidal region of the piles and sea walls

and is due to attacks by the gribble *Limnoria quadripunctata*. Initial attack occurs some months or years after the wood is exposed to the sea water and after the creosote has leached out of the superficial layers. When piles are braced, the notches or bolt holes created during construction often allow the gribbles immediate access to untreated or under-treated wood. Ultimately, the wooden piles are girdled and often severed by massive gribble attack. In the burrows of *Limnoria*, the amphipod *Chelura terebrans* Phillipi, 1839, is often found, but it is uncertain what role this animal plays in the destruction of the wood, if any.

Subtidally, a few *Limnoria* are found in superficial burrows in the wood all the way to the bottom, but little structural damage is done. Throughout this range, however, and especially at the mud line on the bottom, the wooden piles and sea walls are ultimately attacked by the shipworm *Bankia setacea* (Tryon, 1863). The damage is so severe that the piles often break off at the mud line, especially the fender piles. A detailed study on *Bankia setacea* in Monterey Harbor has been published (HADERLIE & MELLOR, 1973).

There is a number of molluscan borers which excavate burrows in the siliceous shale and calcareous stone found in and around Monterey Bay (HADERLIE, 1976). None of these, however, penetrate granite. Most of the aggregate used in the concrete piles under the wharf was granite gravel and these piles appear to have undergone little deterioration as a result of biological action over the past 50 years. So far in our studies we have found no borers in the concrete piles themselves.

In the thick side wall plates of the giant barnacle *Balanus nubilus*, and the upper exposed valves of the rock oyster *Pododesmus cepio*, two common animals on the wharf piles, several boring organisms are found. The most common and destructive is the boring sponge *Cliona celata*. Many of the older barnacles and rock oysters are severely infested with this sponge. In the massive fouling collars surrounding most of the piles in the lowest part of the intertidal area, the large *Balanus nubilus* are often piled up several layers thick, the oldest ones being at the bottom attached directly to the pile. These lower barnacles are often badly eroded by the sponge and so weakened that they collapse and allow massive portions of the collar to fall to the bottom. The sponge is found in the shell plates of both living and dead barnacles, but is more common in the dead shells. In one large living *Balanus nubilus* examined from Pile A at a depth of -4.0 m, the sponge had penetrated through the bases of the lateral parapets but had not bored through the inner mantle layer. Many dead *B. nubilus* shells are also bored by the polychaete *Dodecaceria fowkesi*, and one living barnacle

was infested with these worms that had penetrated to the inner mantle layer. The phoronid *Phoronis vancouverensis* also burrows into the shell plates of *Balanus nubilus* and the upper valve of *Pododesmus cepio*. The only molluscan borers observed were the date mussel (*Lithophaga plumula kelseyi*) and the pholad *Penitella conradi*; in both cases these borers were found in burrows in the wall plates of dead *Balanus nubilus*.

Recolonization of Concrete Piles

One of the objectives of this investigation was to initiate the process of making long-term observations on the piles from which fouling growth had been removed and to record the recolonization of the concrete. These observations will be continued for some years in an attempt to learn how long it takes for a new climax community to become established. The concrete piles subject to the detailed study described above were scraped clean of macroscopic organisms during the period between September 1974 and September 1975. In order to have a fixed starting period for observations on recolonization of the piles, the south faces of all the study piles were again scraped of all fouling growth in November 1975 and the settlement of organisms and gradual recolonization have been monitored regularly from that date until late May 1977. These observations will continue, but we will report here our findings over the initial 18 month period.

On Pile A, the one studied from the highest tide level to the bottom, barnacles settled almost at once, *Balanus glandula* and *Chthamalus dalli* in the high intertidal area, *Tetraclita squamosa rubescens* in the mid-intertidal region, and *Balanus crenatus* subtidally along practically the entire submerged length of the pile. Also throughout the intertidal area *Ulva* spp. soon covered the pile. Within a few weeks mature individuals of the anemones *Anthopleura elegantissima* and *Metridium senile* were present in the mid- and low intertidal region, presumably having moved onto the bare concrete from the north face of the pile that had not been scraped. Subtidally, *Phyllochaetopterus prolifica* colonies were present after 6 months and large solitary *Metridium* were common.

After 18 months the fouling population on Pile A was reestablished in most respects. The major difference between the populations of organisms on the north, undisturbed face of the pile and the south face which was scraped clean of macroscopic growth is the lack of identifiable *Balanus nubilus* on the south face of the pile. Also, the newly established *Phyllochaetopterus* colonies both in the low intertidal area and subtidally are still rather small. High in the intertidal area new *Balanus glandula* are now up to 1.5 cm in basal diameter, and in the mid-

intertidal zone *Tetraclita* up to 1 cm diameter are common. In place of the collar of *Phyllochaetopterus* and associated animals at the 0.0 m tide level and below the pile now has a heavy growth of marine plants including *Ulva* spp., *Gigartina exasperata*, *Neogardhiella baileyi*, *Desmarestia ligulata*, *Dictyoneuropsis reticulata* and *Polyneura latissima*. Subtidally, among the anemones and worm tubes, are large slabs of the ascidian *Aplidium solidum*, and covering nearly everything is a thick growth of the bryozoan *Bowerbankia gracilis*.

The other three study piles were scraped clean only on the south face of each pile in the intertidal area down to the -0.5 tide level, so no subtidal observations during the past 18 months have been made. As in the case of Pile A, the scraped region of Pile B soon exhibited newly settled acorn barnacles and these have thrived, and the anemones *Anthopleura elegantissima* and *Corynactis californica* soon moved from the crowded north face to the south face of the pile. After 18 months the scraped part of the pile still appears sparsely populated, and much of the surface is covered with the encrusting bryozoan *Celleporaria brunnea* and the erect fuzzy *Bowerbankia gracilis*. No barnacles identifiable as *Balanus nubilus* have settled to date.

Pile C never possessed the massive collar of *Balanus nubilus* so characteristic of most piles, although a few isolated individuals were present. After scraping, it slowly accumulated a population of the smaller acorn barnacles and anemones. After 18 months, the south face of this pile has a fouling growth much like the north face except there are no *Balanus nubilus* and the other acorn barnacles are smaller.

Pile D, after being scraped, accumulated a vast number of the small brown barnacles *Chthamalus dalli* in the upper intertidal area, but very few *Balanus glandula*. *Tetraclita squamosa rubescens* settled in the mid-intertidal region and are now 1 cm in basal diameter. The lower part of the intertidal zone is dominated at present with masses of hydroids (especially *Obelia* spp.) and the ascidians *Aplidium solidum* and *Ascidia ceretodes*. Small colonies of *Corynactis californica*, not present before scraping, are now found on the concrete. None of the *Phyllochaetopterus prolifica* colonies have returned to the low intertidal region, and it is this feature, plus the presence of *Corynactis*, that distinguishes the south from the undisturbed north face of this pile.

SUMMARY

1. Monterey Municipal Wharf No. 2 was built 50 years ago on a combination of wooden and concrete pilings. The piles have collected a large and complex community of organisms which have not been subject to detailed study until now.
2. This report reviews the populations of organisms living on the piles and on the sea walls that have been added to the wharf in more recent years. In addition to a general survey of the piles of the entire wharf, a detailed qualitative and quantitative study of the organisms living on a few selected piles is reported on.
3. Since the construction of a marina in 1960, environmental parameters associated with the shoreward part of the wharf have been changed and the populations of wharf piling dwellers on this part of the wharf significantly altered.
4. After removal of all macroscopic fouling growth from the intertidal and subtidal area of selected concrete piles, the recolonization of these piles has been monitored and will be followed until a climax community is reestablished.

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1977. Fouling communities in the intertidal zone of wooden and concrete pilings at Monterey, California. pp. 229-239 in: V. Romanovsky (ed.), Proc. 4th Internat. Congr. Mar. Corrosion and Fouling
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The Chromodoridinae Nudibranchs from the Pacific Coast of America. - Part III. The Genera *Chromolaichma* and *Mexichromis*

BY

HANS BERTSCH¹

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(2 Plates; Text figures 16 to 25)

THE FIRST SEGMENT of this 4-part work (BERTSCH, 1977) examined the methodology of opisthobranch systematics, radular characteristics, and the supra-specific taxonomy of the Chromodorididae. Part II treated the 6 known species of *Chromodoris* from the Pacific coast of America (BERTSCH, 1978a).

Chromolaichma Bertsch, 1977

A suite of characteristics is diagnostic for this new genus of Chromodoridinae nudibranchs with an elongate radula. The number of radular rows is at least 2 - 3 times greater than the maximum number of teeth per half-row; the width : length ratio is greater than 1 : 3. A rachidian may or may not be present. The radular teeth are unicuspid, but denticles tend to remain small and on the outer lateral face throughout the entire tooth row. The outermost lateral teeth are flat blades (often elongate

along the antero-posterior plane), without denticles. The smooth outer teeth exhibit an ontogenetic increase: with larger radulae, there is a greater number of smooth outer lateral teeth.

Type Species: *Casella sedna* Marcus & Marcus, 1967.

Also included: *Chromodoris dalli* Bergh, 1879c; *Chromodoris punctilucens* Bergh, 1890; and *Chromodoris youngbleuthi* Kay & Young, 1969.

Chromolaichma sedna (Marcus & Marcus, 1967)
comb. nov.

(Figures 3-G, 16, 18 - 21, 47 - 50)

References and Synonymy:

- Casella sedna* MARCUS & MARCUS, 1967: 178-181; figs. 34-37
Chromodoris fayae LANCE, 1968: 3-6, figs. 1-5
Glossodoris sedna (Marcus & Marcus). ABBOTT, 1974: 355
Chromodoris sedna (Marcus & Marcus). BERTSCH, 1970: 8.
 BERTSCH, 1971: 16. KEEN, 1971: 822; plt. 20, fig. 5.
 SPHON & MULLINER, 1972: 150-151. SPHON, 1972b:

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Explanation of Figures 51 to 56

Scanning Electron Micrographs of the Radular Teeth of
Chromolaichma dalli and *Mexichromis porterae*

- Figure 51: *Chromolaichma dalli*; jaw elements (HB 38 A) ×3850
 Figure 52: *Chromolaichma dalli*; rachidian and innermost lateral teeth. A fair amount of tooth wear (broken and rounded cusps) is visible (HB 38 A) ×1300
 Figure 53: *Chromolaichma dalli*; outer denticled lateral teeth (HB 38 A) ×1300

- Figure 54: *Chromolaichma dalli*; smooth outermost lateral teeth (HB 38 A) ×1300
 Figure 55: *Mexichromis porterae*; innermost lateral teeth (HB 390 A) ×800
 Figure 56: *Mexichromis porterae*; lateral teeth (HB 390 A) ×800

59. BERTSCH *et al.*, 1973: 289, 292, 293. BERTSCH, 1973: 108. BRUSCA, 1973: 174. KEEN & COAN, 1975: 43. BIRKELAND, MEYER, STAMES, & BUFORD, 1975: 67. BERTSCH, 1976a: 121. BERTSCH, 1975b: 157

Material Examined and Distribution:

Baja California, Gulf coast

- 1) 1 specimen, 12 m subtidal, Bahía de Los Angeles; *leg.* D. K. Mulliner, 17 - 18 May 1975
- 2) 1 specimen, 6 m subtidal, Isla Bargo, Bahía Concepción; *leg.* A. J. Ferreira, 29 July 1974 (CAS)
- 3) 5 specimens, Isla Bargo, Bahía Concepción; *leg.* A. J. Ferreira, 29 July 1974 (HB 371 A - B)
- 4) 3 specimens, Nopolo and Juncalito; *leg.* H. Bertsch, M. Ghiselin, and J. Allen, 27 June 1974 (HB 91 A - C)
- 5) 2 specimens, intertidal, Tizate, 8 km N of Bahía Escondido; *leg.* H. and J. DuShane, 6 February 1971 (LACM A 8530)
- 6) 1 specimen, intertidal, 10 km N of La Paz, road to Pichilingue; *leg.* A. G. Smith and A. E. Leviton, 11 January 1959 (CAS)
- 7) 2 specimens, 2 - 3 m subtidal, Bahía Carisalito; *leg.* H. Bertsch, 23 July 1972
- 8) 1 specimen, N. Isla Cerralvo; *leg.* H. Bertsch, 24 July 1969
- 9) 1 specimen, subtidal, W anchorage, Isla Cerralvo (24° 10' N; 109° 55' W); *leg.* J. H. McLean, P. Oringer and L. Marinovich, 9 April 1966 (LACM 66-25)
- 10) 3 specimens, SW Isla Cerralvo; *leg.* H. Bertsch, 25 July 1972 (HB 18 A - C)
- 11) 1 specimen, 1.6 km N of Cabo Pulmo; *leg.* 17 May 1971, R/V *Searcher* (LACM)
- 12) 1 specimen, Cabo Pulmo; *leg.* C. Gage *et al.*, 25 - 26 May 1971 (HB 386; LACM)

Mainland Mexico:

- 13) 1 specimen, Puerto Peñasco, Sonora; *leg.* H. Bertsch and G. G. Sphon, November 1967
- 14) 8 specimens, Puerto Peñasco; *leg.* H. Bertsch, 15 July 1975 (HB 270 A - H)
- 15) 6 specimens, Puerto Peñasco; *leg.* H. Bertsch, 21 July 1975 (HB 276 A - F)
- 16) 9 specimens, Puerto Peñasco; *leg.* H. Bertsch and P. C. Cook, 22 July 1975
- 17) 18 specimens, Puerto Peñasco; *leg.* H. Bertsch and P. C. Cook, 23 - 24 July 1975 (HB 284 A - S)
- 18) 2 specimens, Puerto Peñasco; *leg.* H. Bertsch, 23 - 29 December 1975 (HB 341, 348)
- 19) 1 specimen, Puerto Peñasco; *leg.* P. Pickens, 1964 (US NM F 909)
- 20) 1 specimen, intertidal, Bahía San Carlos, Sonora; *leg.* R. Poorman, November 1975 (LACM)
- 21) 2 specimens, intertidal, Punta Mita, Nayarit (20° 46' N; 105° 33' W); *leg.* G. G. Sphon 21 - 23 January 1970 (LACM)

Central and South America:

- 22) 1 specimen, 8 - 12 subtidal, N side Isla del Cano, Puntarenas, Costa Rica (8° 43' 15" N; 83° 53' 07" W); *leg.* J. H. McLean and J. Wheeler, 14 - 19 March 1972 (LACM)
- 23) 1 specimen, 6 m subtidal, Isla Siboga, Islas de las Perlas, Panama; *leg.* K. B. Meyer, 20 May 1972 (HB 265)
- 24) 5 specimens, intertidal, 2.4 km E of Darwin Research Station pier, S Isla Santa Cruz, Galápagos Islands; *leg.* K. Koford, 9 February 1964 (CAS)
- 25) 1 specimen, Darwin Research Station, Galápagos Islands (0° 45' 06" S; 90° 15' 38" W); *leg.* G. G. Sphon, March 1971 (HB 268; LACM 71-45)

The type locality of *Chromolaichma sedna* is Puerto Peñasco, Sonora, Mexico.

Its known occurrence is from Puerto Peñasco to the Galápagos Islands. It has been reported from numerous intermediate localities: Bahía San Luis Gonzaga, Isla Angel de la Guarda, Isla Santa Cruz, Isla Cerralvo, and Las Cruces (all Baja California); Guaymas, Sonora; Mazatlán, Sinaloa; Santa Cruz, Nayarit; Tenacatita, Jalisco; Colima; and Costa Rica (LANCE, 1968: 6; SPHON & MULLINER, 1972: 150; BERTSCH *et al.*, 1973: 293). This species had been reported previously from the Galápagos Islands based on only one specimen (SPHON & MULLINER, 1972: 150; lot 25 of this study), so the additional specimens (lot 24) from its southern range extremity are significant.

External Morphology and Coloration:

The largest living specimens measured 48 and 58 mm long (new size records; previously reported greatest length while crawling was 47 mm; cf. LANCE, 1968: 3). Seventy-three specimens measured at Puerto Peñasco (July and December 1975), and Nopolo and Juncalito (June 1974) ranged from 10 - 58 mm total length alive ($\bar{X} = 24.3$ mm).

Body color is pure white. Three color bands surround the notum and foot, an inner opaque white, a middle one of vivid red, and a marginal edging of brilliant yellow. The rhinophores and gills are white basally, with deep red on the distal $\frac{1}{2}$ to $\frac{2}{3}$'s of their length. Gills are usually held erect, often with the free portions waving back and forth (increasing water flow across and oxygen availability to the simply branched gills). KEEN (1971: plt. 20, fig. 5) presents a color photograph of the animal.

Radula:

Despite the common occurrence of *Chromolaichma sedna*, reports of only 2 radular formulae are in the literature (MARCUS & MARGUS, 1967: 180; LANCE, 1968: 5). Table 8 presents radular data and means from 51 additional specimens. The combined radular formula is

Table 8

Radular variation in *Chromolaichma sedna*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row	Maximum number of teeth per half-row
2	—	—	—	130	55	35
3	—	—	—	129	42	13
USNM F 909	—	—	—	120	52	32
18 A	2.99	1.03	1:2.90	98	40	6
18 B	4.13	1.19	1:3.46	100	46	23
18 C	—	—	—	87	43	8
67	4.3	1.15	1:3.74	109	42	20
91 A	6.34	2.06	1:3.08	112	61	26
91 B	5.74	1.82	1:3.15	105	36	14
91 C	4.75	1.82	1:2.61	102	60	15
265	1.58	0.46	1:3.43	71	25	1
268	1.15	0.42	1:2.74	74	25	0
270 A	1.96	0.63	1:3.11	78	29	4
270 B	2.323	0.73	1:3.18	91	38	8
270 C	2.85	0.97	1:2.94	89	37	11
270 D	3.62	1.29	1:2.81	102	46	24
270 E	1.68	0.59	1:2.86	74	28	3
270 F	2.28	0.81	1:2.81	87	36	5
270 G	2.04	0.65	1:3.14	82	39	5
270 H	3.56	1.13	1:3.15	110	43	16
276 A	3.08	0.86	1:3.58	107	33	4
276 B	2.28	0.91	1:2.51	89	37	7
276 C	2.97	0.97	1:3.06	93	41	11
276 D	2.42	0.95	1:2.55	85	39	6
276 F	1.88	0.63	1:3	83	35	2
279 A	2.89	0.93	1:3.11	96	47	15
279 B	2.22	0.75	1:2.96	86	31	3
279 C	2.67	0.79	1:3.38	96	34	3
279 D	4.38	1.41	1:3.11	120	51	35
279 E	3.49	1.11	1:3.14	98	46	19
279 G	2.65	0.89	1:2.98	93	39	14
279 H	2.32	0.85	1:2.73	93	37	3
279 I	3.64	1.21	1:3.01	110	46	12
284 B	4.12	1.45	1:2.84	108	55	28
284 C	5.17	1.66	1:3.11	137	49	30
284 D	2.1	0.81	1:2.59	74	32	8
284 E	3.62	1.05	1:3.45	107	43	17
284 F	3.27	1.01	1:3.24	94	39	4
284 G	1.98	0.79	1:2.51	80	35	3
284 H	2.81	1.01	1:2.78	96	41	2
284 I	3.15	0.99	1:3.18	98	37	3
284 J	1.62	0.61	1:2.66	66	30	2
284 K	2.53	0.85	1:2.98	83	39	2
284 M	2.06	0.81	1:2.54	87	33	6
284 N	2.69	1.03	1:2.61	91	40	2
284 O	2.99	1.03	1:2.9	95	36	3
284 P	3.17	1.23	1:2.58	99	42	9
284 R	2.08	0.71	1:2.93	82	33	1
341	4.52	1.47	1:3.07	89	43	16
348	2.16	0.65	1:3.32	76	28	1
371 A	6.59	2.34	1:2.82	124	70	39
371 B	6.32	1.9	1:3.33	131	62	39
386 C	4.71	1.37	1:3.44	109	46	17
\bar{X}	3.18	1.057	1:3.002	96.698	40.98	11.98
s	1.308	0.4167	0.304	16.41	9.486	10.95

²MARCUS & MARCUS, 1967; ³LANCE, 1968.

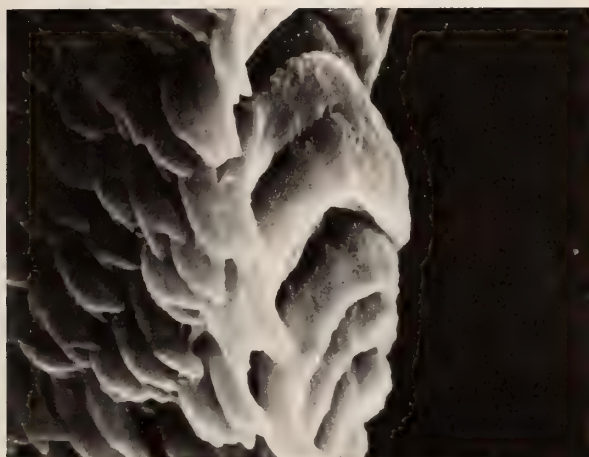


Figure 51

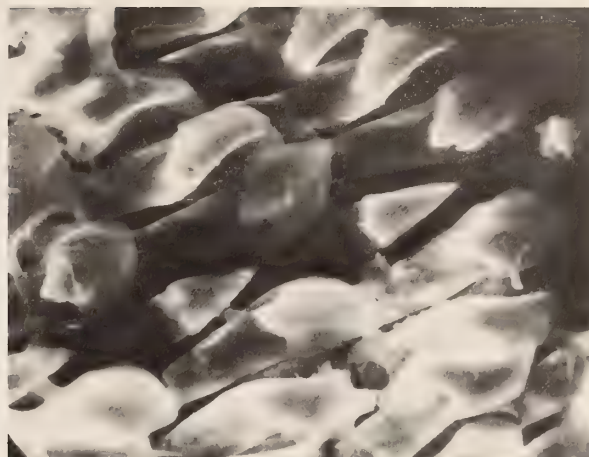


Figure 52



Figure 53



Figure 54



Figure 55

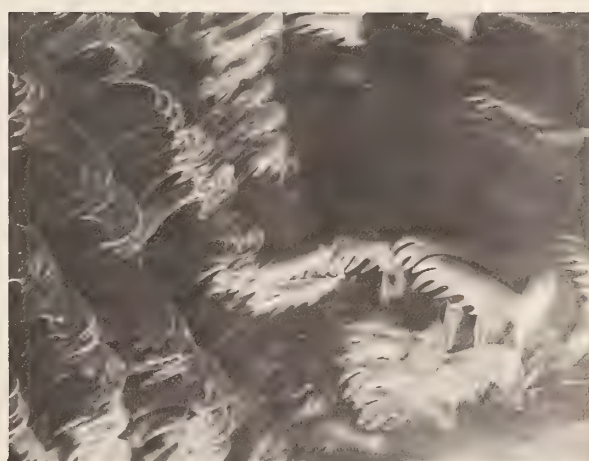


Figure 56

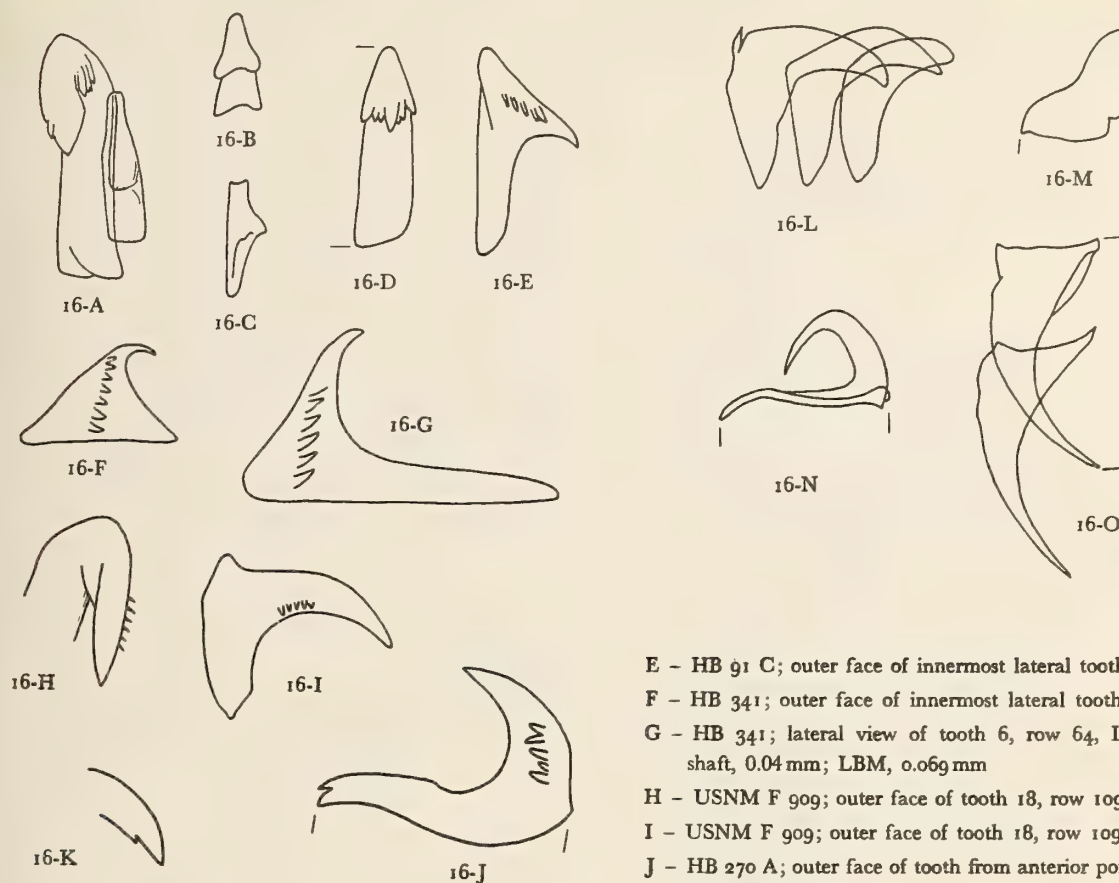


Figure 16

Radular teeth of *Chromolaichma sedna*

- A - USNM F 909; rachidian and innermost lateral teeth, row 109
 B - HB 270 B; rachidian tooth; 0.02 mm long, 0.008 mm wide
 C - HB 91 C; dorso-lateral view of rachidian tooth, row 93
 D - HB 270 C; dorsal view of aberrant rachidian tooth, with 3 accessory denticles on each side of main cusp; row 18; LBM, 0.042 mm

- E - HB 91 C; outer face of innermost lateral tooth, row 93, LSR
 F - HB 341; outer face of innermost lateral tooth, row 37, LSR
 G - HB 341; lateral view of tooth 6, row 64, LSR; length of shaft, 0.04 mm; LBM, 0.069 mm
 H - USNM F 909; outer face of tooth 18, row 109, LSR
 I - USNM F 909; outer face of tooth 18, row 109, LSR
 J - HB 270 A; outer face of tooth from anterior portion of radula; LBM, 0.04 mm
 K - HB 284 B; distal portion of outer lateral tooth with a single denticle
 L - HB 341; 3 outermost lateral teeth, row 36, RSR
 M - HB 341; developing tooth, 2nd from outer edge of radula, penultimate row, RSR; LBM, 0.028 mm
 N - HB 341; developing tooth, 7th from outer edge, penultimate row, RSR; LBM, 0.057 mm
 O - HB 341; developing teeth, 4th (upper) and 5th tooth from outer edge of radula, 3rd last row; LBM, 0.051 mm

66 - 131 (28 - 70 · 1 · 28 - 70). The number of smooth outermost laterals varies from 0 to 39.

Least squares regression analysis proves that the maximum number of teeth per half-row increases with the greater number of tooth rows (Figure 18). The regression line formula is $Y = -2.53 + 0.45 X$. The coefficient of correlation is 0.7783 ($P < 0.001$, $n = 53$).

The number of tooth rows increases with the greater length of the radula (Figure 19). The equation, $Y =$

$63.32 + 9.985 X$, describes the regression line with $r = 0.8594$, $P < 0.001$, and $n = 49$.

The radular width and the maximum number of teeth per half-row are positively correlated (Figure 20); $Y = 18.92 + 20.34 X$, $r = 0.8913$, $P < 0.001$, $n = 49$.

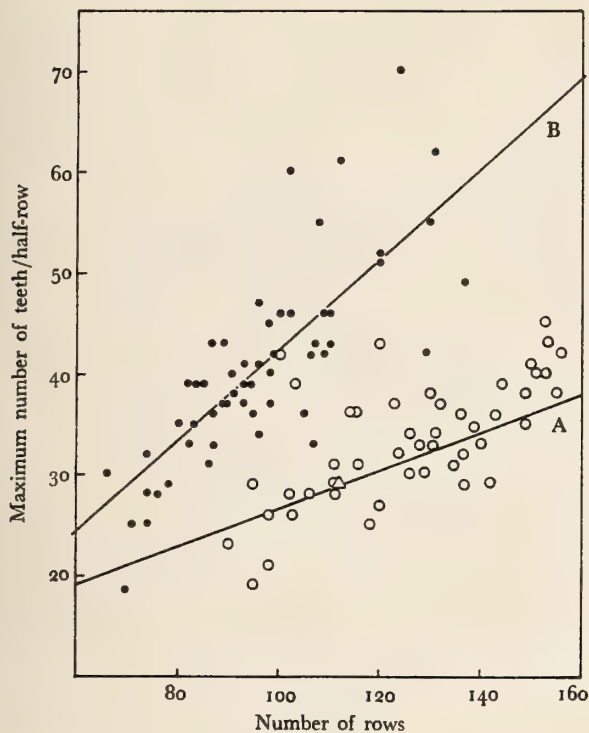
The number of smooth outermost lateral teeth is also dependent on the size of the radula (Figure 21). The number of tooth rows and the maximum number of smooth laterals are positively correlated ($r = 0.8142$, $P < 0.001$,



Figure 17

Radular teeth of *Chromolaichma dalli*

- A - HB 38 B; outline sketch of entire radula, before flat mounting; LBM, 3 mm
- B - HB 285 G; rachidian tooth, 0.016 mm wide
- C - HB 38 B; rachidian tooth
- D - HB 324 C; ventro-lateral view of tooth 2, row 132, RSR
- E - HB 324 C; ventral view of innermost lateral tooth, row 132, LSR
- F - HB 324 B; 3rd lateral tooth, row 1; LBM, 0.075 mm
- G - USNM F 908; 8th lateral tooth, row 59, RSR
- H - USNM F 908; ventro-lateral view, outer face of tooth 12, row 30, RSR
- I - USNM F 908; dorso-lateral view, tooth 14, row 34, RSR
- J - HB 38 B; tooth 16, row 50, RSR
- K - HB 324 C; tooth 17, row 60, LSR; LBM, 0.127 mm
- L - HB 324 C; dorso-posterior view, teeth 8 and 9, approximately row 140, LSR
- M - HB 324 B; tooth 15, row 11, RSR
- N - HB 324 B; tooth 18, row 121, LSR; LBM, 0.056 mm; length of base, 0.069 mm
- O - HB 324 D; an outer lateral tooth, row 46, LSR
- P - USNM F 908; 2nd tooth from outer edge, row 36, RSR
- Q - USNM F 908; outermost lateral tooth, row 38, RSR
- R - HB 324 B; outer lateral tooth, approximately row 30
- S - HB 38 B; outer laterals, teeth 28 - 32, drawn to relative proportion and position, row 50, RSR



(← adjacent column)

Figure 18

Correlation between maximum number of teeth per half-row and number of tooth rows. A. *Chromolaichma dalli* (open circles); B. *Chromolaichma sedna* (dots); open triangle is holotype of *Chromolaichma dalli*

$n = 53$). The regression line formula is $Y = -40.56 + 0.543 X$.

The most anterior portion of the radula is pointed, caused by tooth wear and loss of lateral teeth.

Rachidian tooth is present (Figures 16 A - C, 47); one radula had an aberrant rachidian tooth with 3 small denticles flanking a central cusp (Figure 16 D). The first lateral tooth has 1-4 denticles on the inner face, and 5-8 on the outer face (Figures 16 E - F, 47). Succeeding lateral teeth (Figures 16 G - J, 48) have sharp, recurved shafts. There is an increasing number of denticles on each tooth throughout the first 10 - 20 teeth, and then a decrease in their number until the smooth outermost laterals are reached. Excluding the smooth laterals, denticles on the outer face of lateral teeth from row 34 of specimens HB 270 A and 341 ranged from 2 - 8 ($\bar{X} = 5.4$, $n = 41$). Some radulae may have 9 - 10 denticles on the lateral teeth (Figure 48).

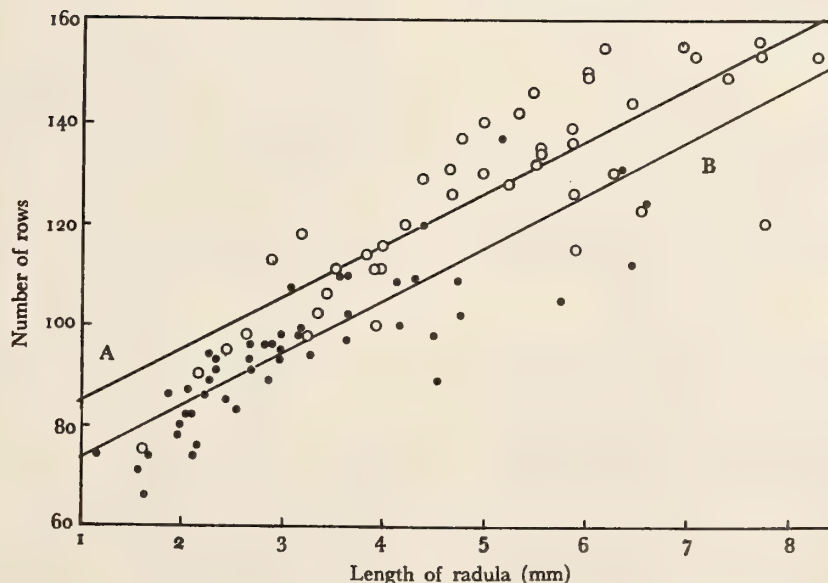


Figure 19

Relation between number of tooth rows and length of radula, *Chromolaichma dalli* and *Chromolaichma sedna*. Symbols as in Figure 18

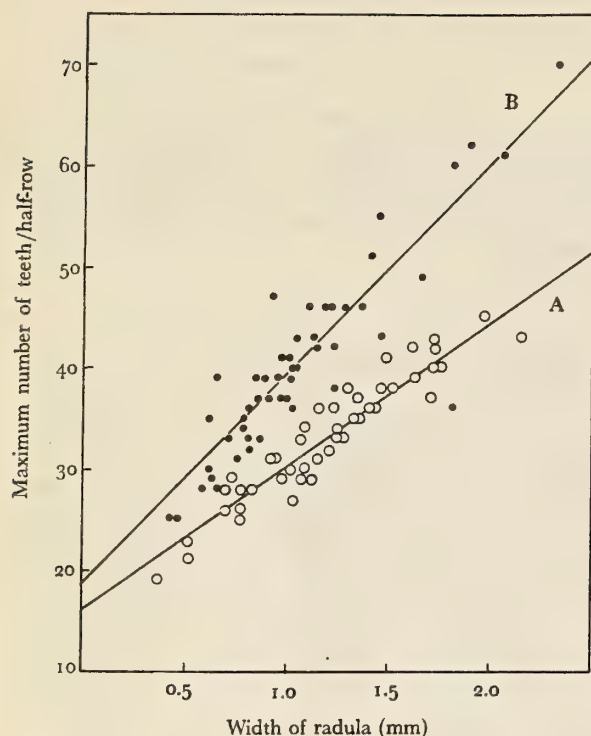


Figure 20

Correlation between maximum number of teeth per half-row and width of radula, *Chromolaichma dalli* and *Chromolaichma sedna*. Symbols as in Figure 18

Figure 49 illustrates the transition zone between denticles and smooth teeth. There is a reduction in the number and prominence of denticles; the shaft of the tooth is still hook-like, but very shortly the following lateral teeth become blade-like (Figures 16-L and 45). The outermost teeth in 2 radulae had a slight notch (almost a small denticle) just below the cusp (Figure 16-K).

The length of the cusps of the denticled teeth across a half-row (specimen HB 341) varied from 0.012-0.038 mm ($\bar{X} = 0.0235$ mm, $n = 19$). The small size of the lateral denticles is shown by the ratio of lengths of the first denticle : cusp. The cusp ranged from 6.67 to 19 times longer than the first denticle ($\bar{X} = 8.99$, $s = 3.396$, $n = 19$).

Figure 16 M - O illustrates developing lateral teeth. As growth proceeds, the tooth increases in length and thickness (strength) of the shaft.

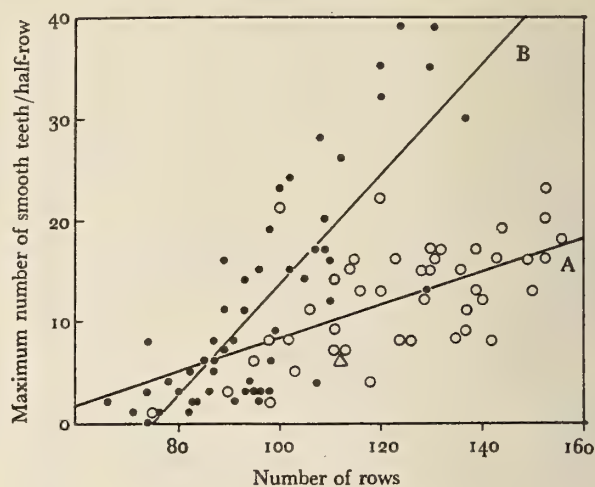


Figure 21

Correlation of maximum number of smooth teeth per half-row and number of tooth rows, *Chromolaichma dalli* and *Chromolaichma sedna*. Symbols as in Figure 18

Discussion:

Chromolaichma sedna was originally named in the genus *Casella*; later transferral to the genus *Chromodoris* was appropriate at that time given the understanding of the latter 2 genera. Now, however, with the examination of many radulae from all the known Chromodoridinae species from the American Pacific, the data indicate clearly that a new genus should be established to accommodate this species and other similar species. This new genus is not monotypic, but encompasses at least 3 (probably 4) species; moreover, the generic diagnosis is based on a suite of characteristics that affect the entire radula, and are readily differentiable from other nudibranch genera.

Chromolaichma dalli Bergh, 1879, *comb. nov.*

(Figures 3-H, 18 - 21, 51 - 54)

References and Synonymy:

- Chromodoris dalli* BERGH, 1879c: 72, 109-112. BERGH, 1878c: 3 (*nomen nudum*). BERGH, 1879a: 3 (*nomen nudum*). BERGH, 1880: plt. 13, figs. 1-7; plt. 14, figs. 1-4. BERGH, 1891: 141. BERGH, 1892: 118. BERGH, 1898: 533. COCKERELL & ELIOT, 1905: 36. MAC-

- FARLAND, 1906: 129. MACFARLAND, 1966: 154; plt. 34, figs. 10-11. MARCUS & MARCUS, 1967: 176. SPHON, 1972b: 59. BLOOM, 1976: 292. BERTSCH, 1976b: 158.
- Glossodoris dalli* (Bergh). O'DONOGHUE, 1926: 211. PRUVOT-FOL, 1951a: 95-96. STEINBERG, 1963: 69. ABBOTT, 1974: 355.
- Chromodoris banksi* FARMER, 1963: 84; plt. 1 b; text figs. 1 f-k. FARMER, 1967: 341. MARCUS & MARCUS, 1967: 175-176, 237. SKOGLUND, 1970: 429. BERTSCH, 1970: 8. KEEN, 1971: 822. SPHON, 1972a: 5 (color photograph). SPHON, 1972b: 59. BERTSCH *et al.*, 1973: 287-289, 292. KEEN & COAN, 1975: 43. BERTSCH, 1976b: 157.
- Glossodoris banksi* (Farmer). ABBOTT, 1974: 355.
- Chromodoris banksi sonora* MARCUS & MARCUS, 1967: 173 to 176; figs. 25-29; 237. KEEN, 1971: 822, fig. 2329.
- Chromodoris sonora* MARCUS & MARCUS. SPHON, 1972b: 53, 59.
- Chromolaichma dalli* (Bergh). BERTSCH & MEYER, in prep.

BERTSCH *et al.* (1973) synonymized *Chromodoris banksi sonora* Marcus & Marcus with *C. banksi* Farmer. The new synonymization of *banksi* with *dalli* will be substantiated in the discussion of *Chromolaichma dalli*.

Material Examined and Distribution:

Pacific coast of Baja California:

- 1) 1 specimen, Man-of-War Cove, Bahía Magdalena (24° 37.5'N; 112° 7.5'W); leg. J. H. McLean and F. LaFollette, 31 October 1971 (LACM 71-183)

Gulf coast of Baja California:

- 2) 2 specimens, 1.6 km N of Puertocitos; leg. H. Bertsch, T. Gosliner & G. Williams, 29 March 1972.
- 3) 5 specimens, intertidal, N end of "Turtle Pen," Isla Coronado, Bahía de Los Angeles; leg. G. G. Sphon and D. Mulliner, May 1976 (LACM)
- 4) 2 specimens, 12-18 m subtidal, on reef between Islas Calaveras and Smith, Bahía de Los Angeles; leg. D. Mulliner, May 1976 (LACM)
- 5) 1 specimen, Isla San Marcos (25° 30'N; 111° W); leg. E. Janss, Jr., April 1974 (LACM)
- 6) 1 specimen, 22 km S of Mulege; leg. H. Bertsch and B. Rose, 21 December 1973 (HB 37)
- 7) 2 specimens, 22 km S of Mulege; leg. H. Bertsch and B. Rose, 21 December 1973 (HB 38 A-B)
- 8) 1 specimen, Punta Aguja, mouth of Bahía Concepción; leg. A. J. Ferreira, 28 July 1974 (HB 364)
- 9) 1 specimen, Coyote Cove, Bahía Concepción; leg. D. Mulliner, 19-20 May 1975
- 10) 1 specimen, subtidal, Nopolo (Loreto area); leg. H. Bertsch, 27 June 1974 (HB 90)
- 11) 1 specimen, Arrecife San Marcial, S of Puerto Escondido; leg. A. J. Ferreira, 15 June 1974 (HB 365)

- 12) 1 specimen, intertidal, Isla San Francisco; leg. G. G. Sphon, 1 April 1974 (HB 385; LACM)
- 13) 1 specimen, Los Islotes; leg. A. J. Ferreira, 16 August 1973 (HB 374)
- 14) 1 specimen, middle of E side of Isla Espíritu Santo; leg. A. J. Ferreira, 19 August 1973 (CAS)
- 15) 2 specimens, intertidal, 6 km N of La Paz; leg. A. G. Smith and A. E. Leviton, January 1959 (CAS)
- 16) 6 specimens, intertidal, 9.6 km N of La Paz; leg. A. G. Smith and A. E. Leviton, January 1959 (CAS)

Mainland Mexico:

- 17) 2 specimens, Puerto Peñasco; leg. S. S. Berry, 8-9 March 1949 (CAS)
- 18) 1 specimen, Puerto Peñasco; leg. P. Pickens, 1964/1965 (USNM F 908)
- 19) 1 specimen, intertidal, Puerto Peñasco; leg. H. Bertsch and G. G. Sphon, November 1967
- 20) 1 specimen, Puerto Peñasco; leg. D. Mulliner, December 1970
- 21) 3 specimens, Puerto Peñasco; leg. H. Bertsch, 21 July 1975 (HB 275 A-C)
- 22) 6 specimens, Puerto Peñasco; leg. H. Bertsch, 22-23 July 1975 (HB 278 A-F)
- 23) 10 specimens, Puerto Peñasco; leg. H. Bertsch and P. C. Cook, 24-26 July 1975 (HB 285 A-J)
- 24) 2 specimens, Puerto Peñasco; leg. H. Bertsch, 28 July 1975 (HB 290 A-B)
- 25) 7 specimens, Puerto Peñasco; leg. H. Bertsch and P. C. Cook, 5-9 August 1975 (HB 297 A-G)
- 26) 2 specimens, Puerto Peñasco; leg. H. Bertsch and S. Pohlman, 18-20 August 1975 (HB 305 A-B)
- 27) 2 specimens, Puerto Peñasco; leg. H. Bertsch and S. Pohlman, 21 August 1975 (HB 312 A-B)
- 28) 6 specimens, Puerto Peñasco; leg. P. Pickens, various dates (HB 324 A-F; USNM 753562)
- 29) 1 specimen, Puerto Peñasco; leg. H. Bertsch, 27 December 1975 (HB 349)
- 30) 1 specimen, 9 m subtidal, Bahía San Carlos; leg. A. J. Ferreira, August 1972 (HB 373)
- 31) 3 specimens, intertidal, Bahía San Carlos; leg. R. Poorman, November 1975 (LACM)
- 32) 1 specimen, La Cruz, Nayarit; leg. R. Poorman, 3 January 1976 (LACM)
- 33) 3 specimens, Jalisco; leg. R. Poorman, January 1976 (LACM)

Previous collecting records have been throughout the Gulf of California and in Costa Rica (BERTSCH *et al.*, 1973: 289). The specimen from Bahía Magdalena (lot 1) represents the first record of *Chromolaichma dalli* from the Pacific coast of Baja California; the specimens from southern Mexico (lots 32 and 33) are intermediate localities between the southern Gulf of California and Costa Rica.

Table 9

Radular variation in *Chromolaichma dalli*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row	Maximum number of smooth teeth per half-row
⁴	—	—	—	124	32	8
USNM F 908	—	—	—	103	39	5
⁵	6.0	1.5	1:4	150	41	13
37	3.82	1.17	1:3.26	114	36	15
38 B	5.88	1.41	1:4.17	115	36	16
90	7.77	2.16	1:3.597	120	43	22
275 A	5.31	1.13	1:4.69	142	29	8
275 B	5.49	1.35	1:4.07	132	37	17
275 C	2.42	0.73	1:3.32	95	29	6
278 A	3.92	1.62	1:2.42	100	42	21
278 B	5.47	1.23	1:4.45	143	36	16
278 C	4.97	1.25	1:3.98	130	33	15
278 D	6.44	1.64	1:3.93	144	39	19
278 E	3.19	0.77	1:4.14	118	25	4
285 A	5.86	1.25	1:4.69	126	34	15
285 B	7.39	1.8	1:4.11	149	38	17
285 C	3.535	0.707	1:5	111	28	9
285 D	4.36	1.09	1:4	129	30	12
285 E	4.99	1.07	1:4.66	140	33	12
285 F	5.555	1.212	1:4.58	137	32	11
285 G	7.7	1.74	1:4.43	156	42	18
285 H	2.89	0.707	1:4.09	113	26	7
285 I	4.65	1.09	1:4.27	131	34	16
285 J	3.96	0.99	1:4	111	29	7
290 A	5.21	1.29	1:4.04	128	33	15
290 B	5.555	1.15	1:4.83	135	31	8
297 A	4.67	1.01	1:4.62	126	30	8
297 B	4.2	1.03	1:4.08	120	27	13
297 C	5.84	1.33	1:4.39	139	35	13
297 D	3.98	0.91	1:4.37	116	31	13
297 E	3.43	0.83	1:4.13	106	28	11
297 F	6.0	1.37	1:4.38	149	35	16
297 G	6.26	1.47	1:4.26	130	38	17
305 A	3.33	0.77	1:4.32	102	28	8
305 B	4.77	1.07	1:4.46	137	29	9
312 A	3.23	0.77	1:4.19	98	26	8
324 A	5.86	1.43	1:4.1	136	36	—
324 B	7.07	1.74	1:4.06	153	43	23
324 C	6.18	1.52	1:4.07	155	38	—
324 D	6.95	1.76	1:3.95	151	40	—
324 F	8.26	1.74	1:4.75	153	40	16
349	2.16	0.51	1:4.24	90	23	3
364	1.6	0.36	1:4.44	75	19	1
365	7.72	1.98	1:3.9	153	45	20
373	3.9	0.95	1:4.11	111	31	14
374	6.54	1.72	1:3.8	123	37	16
385	2.65	0.51	1:5.2	98	21	2
\bar{X}	5.043	1.219	1:4.19	125.89	33.34	12.34
s	1.634	0.414	0.467	19.734	6.07	5.451

⁴FARMER, 1963; ⁵MARCUS & MARCUS, 1967.

External Morphology and Coloration:

Reported lengths of living *Chromolaichma dalli* are 15, 24, 33 mm. Twenty specimens that I measured varied from 14 to 46 mm long ($\bar{X} = 27.5$ mm), including specimens 37, 38, 39, and 43 mm long. Notal and foot background color is white. Brown-black spots of varying size are on the notum and sides of the body. Larger specimens tend to have more numerous, smaller black dots, and the background becomes grayish around the center of the dorsum. Cream-colored and occasionally orange (red in larger specimens) spots are mixed among the blackish dots on the notum. Gills and rhinophores are white, tipped orange or light red distally. The color variation between small and large animals is shown by the photographs in FARMER (1963) and SPHON (1972a).

Radula:

Data from the literature and my own investigation are in Table 9. The combined radular formula is 75 - 156 (19 - 45 · 1 · 19 - 45). There are from 1 - 22 smooth outermost lateral teeth. Data from BERGH (1879c: 112 tooth rows, 29 teeth per half-row, with 6 smooth teeth per half-row) were not used in the regression analysis, but are plotted in the graphs (Figures 18 - 21).

The maximum number of teeth per half-row is dependent on the number of tooth rows (Figure 18). The regression formula is $Y = 7.61 + 0.204 X$ ($r = 0.664$, $P < 0.001$, $n = 47$).

The radular length and number of tooth rows (Figure 19) are positively correlated ($Y = 74.18 + 10.36 X$; $r = 0.8525$, $P < 0.001$, $n = 45$).

A positive correlation exists between the radular width and the maximum number of teeth per half-row (Figure 20). The regression line formula is $Y = 16.09 + 14.08 X$; $r = 0.9471$, $P < 0.001$, $n = 45$).

The number of smooth outer lateral teeth per half-row is dependent on the number of tooth rows (Figure 21). The equation $Y = -8.89 + 0.17 X$ describes the regression line ($r = 0.6083$, $P < 0.001$, $n = 44$).

Comprehensive jaw and radular descriptions are in BERGH (1879c: 111) and MARCUS & MARCUS, (1967: 175). Jaw elements are bent rods, bifurcated at the inner end (Figure 51).

Figure 17 A illustrates an entire radula before flattening. A rachidian tooth is present, with a triangular cusp that subtends an acute angle with the base anteriorly, and a right angle posteriorly. The postero-dorsal edge of the cusp varies between being smoothly concave (FARMER, 1963: fig. 1 k), to deeply concave with a median point (Figure 17 B), slightly concave with a median notch

(Figure 52; cf. also BERGH, 1880: plt. 13, fig. 11; plt. 14, fig. 2) to slightly convex with either a median prominence (Figure 17 C), or a median prominence flanked by a similar prominence on each side (MARCUS & MARCUS, 1967: 174; fig. 28 R). Inner lateral teeth (Figure 52) have up to 9 - 10 denticles on the outer face (Figure 17 D - L) increasing in number towards the middle of the denticled teeth, then decreasing closer to the smooth outermost teeth. Laterals near the outer smooth denticles sometimes have denticles on their posterior surfaces (Figure 53 and 17 M - N). Outermost lateral teeth are smooth, lacking denticles, and flattened along the antero-posterior plane (Figures 54 and 17 O - S).

The length of the cusp increases the farther the tooth is from the innermost part of the half-row. The cusp length averaged 0.0176 mm (range, 0.006 - 0.03 mm; $n = 18$). The length ratios of first denticle : cusp averaged 1 : 11.9 (range, 4 - 30; $n = 18$, $s = 7.735$).

Discussion:

Since coloration is an essential characteristic to classify chromodorid nudibranchs, new taxa should be erected only after having observed the living animal. Bergh described *Chromolaichma dalli* based only on preserved material. I have seen numerous specimens of authentic *Chromodoris banksi* that match Bergh's description. Although the color will often fade in preservative solutions, preserved specimens of this species retain for some time hints of the original colors in life. Because of this, one can state that there are no color differences between the 2 nominal species.

The radula is even more diagnostic. The morphology is identical (compare Bergh's, the Marcus's, Farmer's and my figures), and the meristic characters also match. In the relation of number of tooth rows to maximum number of teeth per half-row Bergh's specimen plots right in the middle of the *Chromodoris banksi* specimens (Figure 18). A similar situation holds for the relation between the number of tooth rows and the maximum number of smooth outermost teeth per half-row.

MARCUS & MARCUS (1967: 176) state that *dalli* is related to their new subspecies, but that "the total of 15 branchial plumes, and the rachidian pseudo-tooth divided into two halves by a longitudinal groove, separate *dalli* from *banksi sonora*." Their subspecies has been suppressed; the original description of *Chromodoris banksi* was of specimens with 9 gills. The range of variation of *C. banksi* gills is from 9 - 34. Bergh's specimen lies well within this range, so that the number of branchial plumes cannot give evidence of 2 different species. Differences in the rachidian tooth are also within the range of intraspecific variation (cf. radula description above).

There are no specific differences between Bergh's *Chromodoris dalli* and Farmer's *C. banksi*. Therefore, I propose that *Chromodoris banksi* is a junior subjective synonym of the older *Chromolaichma dalli*.

Bergh described *Chromolaichma dalli* from the Puget Sound area of Washington. However, no further specimens have ever been reported from the coasts of California, Oregon, Washington, nor Canada. The collection of the Friday Harbor Marine Laboratories (in the Puget Sound area) contains no specimens of *C. dalli* (Dr. Eugene Kozloff, personal communication). The Chromodoridinae is a tropical group, which gives strong zoogeographical evidence against the correctness of Bergh's locality data. Bergh's specimen had probably come from the Gulf of California, but was mislabeled. Such a situation is not uncommon in the older literature (MAYR, 1969: 375-377; EMERSON & JACOBSON, 1976: 9, 119). As first reviser, I propose that the type locality of *Chromodoris dalli* Bergh, 1879, be changed to 2.3 miles (3.68 km) south of Puerto-citos, and thereby reflect the correct distribution of this species. This type locality corresponds to that given for *Chromodoris banksi* by FARMER (1963).

Discussion of *Chromolaichma*

The 2 species of *Chromolaichma*, *C. sedna* and *C. dalli*, can be readily separated on the basis of external coloration. *Chromolaichma sedna* is pure white, with 3 marginal color bands; *C. dalli* is covered with numerous blackish dots, with an orange band around the notal edge.

Table 10

Results of t-tests conducted between the species of American Pacific coast *Chromolaichma*.

Numbers are significance probabilities (P).

N.S.: not significant, no difference between the species for the particular measurement or count.

<i>Chromolaichma:</i>	
<i>dalli</i>	<i>sedna</i>
Rows/teeth	<0.001
Length/rows	N.S.
Width/teeth	N.S.
Rows/smooth teeth	<0.001
Length	<0.001
Width	N.S.
W:L ratio	<0.001
Rows	<0.001
Max. teeth	<0.001
Smooth teeth	N.S.

Radular meristic characters differ significantly (Table 10). The means used to calculate the t-tests are given in Tables 8 and 9. The radula of *Chromolaichma dalli* is longer and has more tooth rows than *C. sedna*. These are not ontogenetic differences because the maximum number of teeth per half-row (a meristic quality that increases dependent upon the larger number of tooth rows for each species) is smaller in *C. dalli* and both species have the same maximum number of smooth outermost laterals per half-row.

Mexichromis Bertsch, 1977

Distinct radular tooth morphology characterizes this new genus. The radular teeth are acuspid, with pectinate denticulation (Figures 1 C, 22, 55 and 56; MACFARLAND, 1966: plt. 34, figs. 24, 25, 27, 28). This group is unique, because the distal portion of the shaft does not have a strong cusp that is longer and thicker than the succeeding denticles. The distal structure should be termed a denticle, since it is equal in length and thickness (or shorter and thinner) than some of the succeeding denticles. This is not a character affecting just a few innermost nor outermost lateral teeth, but is a pattern that can be seen throughout the majority of the radula. Moreover, the acuspidate shape is not a minor morphological trait, but a major structural and functional change. The strong rasping or gauging cusp is absent, replaced by a series of picking or sawing points (narrow, elongate denticles).

Type Species: *Chromodoris antonii* Bertsch, 1976

Also included: *Chromodoris porterae* Cockerell, 1901, and *Chromodoris tura* Marcus & Marcus, 1967.

During recent years, the latter 2 species have had frequently changing taxonomic placements. MARCUS & MARCUS (1967: 56) comment on the difficulty of generically classifying their new species. Establishing this new genus resolves the either-or alternatives by recognizing the uniqueness of, and relationships between, these 3 species.

Mexichromis antonii (Bertsch, 1976b), *comb. nov.*

(Figures 3-I, 22 A, 23 - 25)

Synonymy and Reference:

Chromodoris antonii BERTSCH, 1976b: 156-158; figs. 1-8

Material Examined and Distribution:

1) 1 specimen, Isla Alcatraz, Costa Rica (9°50'N; 84°53'W); leg. A. J. Ferreira, February 1972 (identified from a color transparency)

Type Locality:

The type locality is Punta Aguja (near Mulege), Baja California. *Mexichromis antonii* also has been collected subtidally to 28m from Isla San Jose and Los Islotes in the Gulf of California, and in Santiago Bay, near Manzanillo, Colima, Mexico. This new record extends the known range 2100 km southeast.

External Morphology and Coloration:

Lengths of preserved specimens vary from 3 - 4.5 mm; one specimen was 10 mm long while actively crawling.

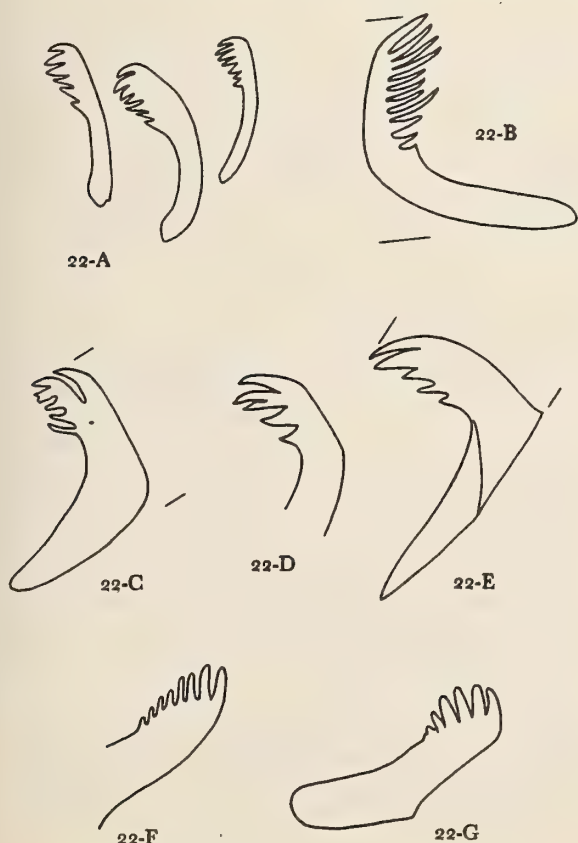
Coloration consists of shades of blue, magenta, black, yellow-orange and white. A complete yellow-orange line encircles the rim of the notum; a black line immediately borders the entire inner side of the yellow-orange band. A wide area of light blue covers the rest of the lateral notal region. This zone is divided by a blackish line concentric with the 2 outermost bands. The central dorsal region (from between the rhinophores to the anterior and lateral sides of the gills) bears a light magenta color, with darker splotches scattered randomly. Running lengthwise down the center of the notum is a thick, broken white

line, bordered by a slight yellowish tinge. Rhinophores are light magenta proximally, and black the distal $\frac{1}{2}$ of their length. The 6 or 7 pinnate gill plumes are pinkish-white basally, each tipped with black. Rim of branchial pouch is tinged yellowish. The dorsal portion of the foot, extending past the mantle, is rimmed by black, with successive light blue and dark blue regions, with a small broken white line along its center.

Radula:

The approximate radular sizes and formulae of 3 specimens are plotted in Figures 23 - 25. The combined radular formula is approximately 54 - 78 (32 - 41 · 0 · 32 - 41). There are not enough specimens available to calculate regression line formulae.

The radula has no rachidian tooth. The lateral teeth (Figure 22 A) bear long denticles, approximately $\frac{1}{2}$ the total width of the erect hook along an antero-posterior plane. There is no prominent cusp thicker and larger than the succeeding denticles. Instead, this structure is reduced to approximately the same size and thickness as the denticles, and it is often actually shorter than the immediately adjacent denticle. The inner teeth of each half-row have 4 denticles. The innermost tooth does not appear to have additional denticles on its inner face. In the central portion of each half-row the teeth have 6 - 7 (sometimes 8) denticles. The outermost lateral teeth have only 4 or 5 denticles. All the teeth have a base not clearly set off from the erect denticular shaft; the postero-dorsal surface of the tooth curves evenly upwards from the posterior portion



(← adjacent column)

Figure 22

Mexichromis: radular teeth

- A - *Mexichromis antonii*: 3 lateral teeth (after BERTSCH, 1976b)
 B - *Mexichromis porterae*: HB 255 A; lateral tooth, LBM, 0.03 mm
 C - *Mexichromis porterae*: HB 255 B; lateral tooth, LBM, 0.024 mm
 D - *Mexichromis porterae*: HB 255 B; distal shaft of lateral tooth
 E - *Mexichromis porterae*: HB 390 A; 2nd lateral tooth, row 23, RSR; LBM, 0.026 mm; length of base, 0.04 mm
 F - *Mexichromis tura*: USNM, F 809 (holotype); distal shaft, lateral tooth $\frac{2}{3}$ the distance between center of radula and outer edge, approximately row 15
 G - *Mexichromis tura*: USNM, F 809; outermost tooth, approximately row 7

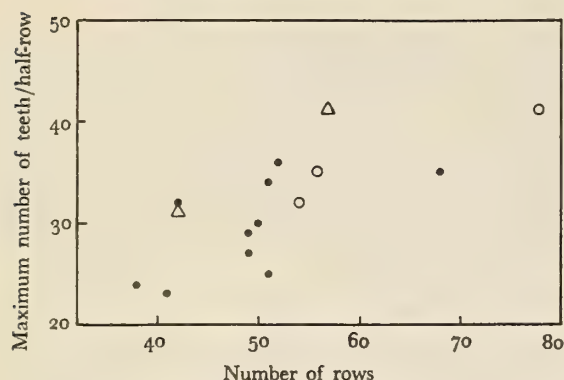


Figure 23

Relation between maximum number of teeth per half-row and number of tooth rows, *Mexichromis porterae* (dots), *Mexichromis antonii* (open circles) and *Mexichromis tura* (open triangles)

of the base; outer teeth have a very short base. Scanning electron micrographs of the radula appear in BERTSCH (1976b: figs. 3-8).

Discussion:

BERTSCH (1976b) gives diagnostic separations of this rare species from other American Pacific Chromodoridinae.

Mexichromis porterae (Cockerell, 1901), *comb. nov.*

(Figures 3-J, 22 B-E, 23-25, 55-56)

References and Synonymy:

- Chromodoris porterae* COCKERELL, 1901: 79. COCKERELL, 1902: 20. MACFARLAND, 1905: 44-45. MACFARLAND, 1906: 129; pl. 26, figs. 13-14. GUERNSEY, 1912: 74 to 75; fig. 39 B. JOHNSON & SNOOK, 1927: 494. MACFARLAND, 1966: 163-165; pl. 24, figs. 4-5; pl. 34, figs. 24-31. BERTSCH & FERREIRA, 1974: 344. SMITH & CARLTON, 1975: 528-529, 538. BERTSCH, 1976b: 158.
- Glossodoris porterae* (Cockerell). O'DONOGHUE, 1926: 212. O'DONOGHUE, 1927: 91-92. SMITH & GORDON, 1948: 180. PRUVOT-FOL, 1951b: 134. LANCE, 1961: 66. STEINBERG, 1963: 70. SPHON & LANCE, 1968: 79. RICKETTS & CALVIN, 1968: 119, 514. ABBOTT, 1974: 355; pl. 17, fig. 4252.
- Hypselodoris porterae* (Cockerell). ROLLER & LONG, 1969: 425, 429. LANCE, 1969: 37. ROLLER, 1970a: 371. SPHON, 1972b: 65. BERTSCH *et al.*, 1973: 287.

Material Examined and Distribution:

California:

- 1) 1 specimen, Pacific Grove; *leg.* F. M. MacFarland, no date (HB 440; CAS)
- 2) 2 specimens, subtidal, Santa Cruz Island; *leg.* A. J. Ferreira, 11 July 1975 (HB 362 A-B)
- 3) 2 specimens, 12 m subtidal, La Jolla kelp beds; *leg.* J. H. McLean, 9 September 1972 (HB 389 A-B; LACM 72-110)
- 4) 2 specimens 21-24 m subtidal, Isla Coronado; *leg.* A. J. Ferreira, 28 September 1973 (HB 255 A-B)

Baja California, Mexico:

- 5) 3 specimens, subtidal, Sacramento Reef, S of Isla Geronimo (29°48'N; 115°48'W); *leg.* A. J. Ferreira, 26 September 1973 (HB 254 A-C)
- 6) 1 specimen, 6-12 m subtidal, Sacramento Reef; *leg.* J. H. McLean, 26-27 September 1971
- 7) 3 specimens, 24 m subtidal, SW of Isla Natividad, approximately 20 km S of Isla Cedros (27°52'N; 115°12'40"W); *leg.* J. H. McLean and P. LaFollette, 22 October 1971 (HB 390 A-C; LACM 71-165)
- 8) 1 specimen, Baja California; R/V *Searcher*, 1971 (HB 391; LACM A 8500)

Type Locality:

The type locality of *Mexichromis porterae* is La Jolla, California; the range of the species is from Monterey, California, to the vicinity of Isla Cedros, Baja California (lot 7, from SW of Isla Natividad, is the southernmost known record). Intermediate collecting records are Santa Barbara County (SPHON & LANCE, 1968), Laguna Beach (GUERNSEY, 1912), and San Diego (MACFARLAND, 1966).

External Morphology and Coloration:

Length of living specimens is usually 10-20 mm (largest, 28.2 mm; MACFARLAND, 1966: 165). Body color is a deep ultramarine blue (illustrated in MACFARLAND, 1966, and LANCE, 1969). Dorsum has 2 longitudinal bright orange (or yellow) stripes that end anteriorly at the rhinophores, and a single bright orange (or yellow) crescent-shaped stripe anterior to the rhinophores. A median light blue line extends from between the rhinophores to the anterior edge of the branchial pocket; mantle margin is rimmed with a narrow white band. There are approximately 9 to 12 branchial plumes; rhinophores and gills are bluish, lighter basally than distally.

Radula:

There is only one, incomplete, description of a *Mexichromis porterae* radula in the literature (MACFARLAND,

1966: 164). The data from 10 radulae are presented in Table 11. The combined radular formula is 38 - 68 (23 -

istic is exceptionally well illustrated by MACFARLAND, (1966: plt. 34, figs. 24, 25, 27, and 28), who also wrote (*op. cit.*: 164) that "the teeth are lamellate, bifid at the summits, their bases long, much compressed, hooks den-

Table 11

Radular variation in *Mexichromis porterae*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
254 B	0.848	0.299	1:2.84	51	25
254 C	0.558	0.162	1:3.44	41	23
262 A	0.654	0.234	1:2.79	38	24
262 B	0.856	0.267	1:3.21	49	27
389 A	0.865	0.283	1:3.06	50	30
389 B	0.808	0.283	1:2.86	49	29
390 A	1.333	0.695	1:1.92	52	36
390 B	1.27	0.63	1:2.02	68	35
391 A	0.913	0.533	1:1.71	51	34
391 B	0.824	0.259	1:3.18	42	32
\bar{X}	0.893	0.365	1:2.703	49.1	29.5
s	0.2407	0.1839	0.603	8.25	4.696

36 · 0 · 23 - 36); there is no rachidian tooth (agreeing with MACFARLAND's, *loc. cit.*, statement, "As clearly as can be made out there is no median plate").

Because of both the small number of available specimens that I examined, and the range of variation, no correlation was statistically proven between the number of tooth rows and the maximum number of teeth per half-row ($r = 0.629$, $P < 0.1 > 0.05$). The data are plotted in Figure 23.

A positive correlation was proven between the length of the radula and the number of tooth rows (Figure 24). The regression line formula is $Y = 24.8 + 27.22 X$; $r = 0.7939$, $P < 0.01$, $n = 10$.

Similarly, a positive correlation exists between the width of the radula and the maximum number of teeth per half-row (Figure 25). The equation is $Y = 21.51 + 21.93 X$; the coefficient of correlation is 0.8588 ($P < 0.01$, $n = 10$).

The radula and its teeth are extremely small. The morphology of innermost lateral teeth (Figures 55 - 56) approaches a *Hypselodoris*-shape, but the first 2 denticles are not developed as much, and the first denticle is not the large, dominant cusp of *Hypselodoris*. Lateral teeth (Figures 22 B - E) vary in shape. The distal shaft ends consistently with a pointed denticle smaller than or equal in size to the succeeding denticles. This unique generic character-

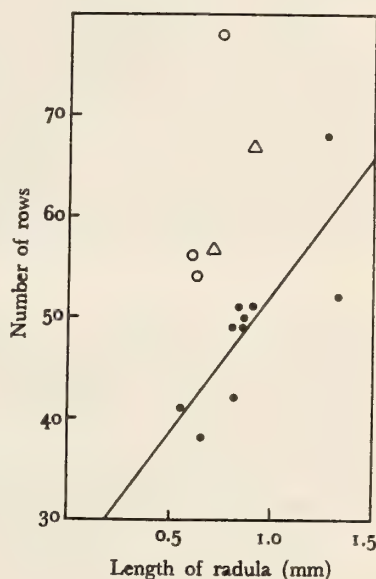


Figure 24

Correlation between number of tooth rows and length of radula, *Mexichromis porterae* (calculated regression line), *Mexichromis antonii*, and *Mexichromis tura*. Symbols as in Figure 23

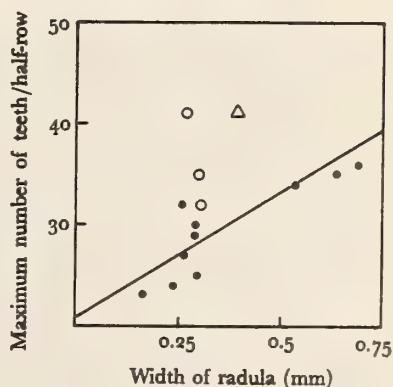


Figure 25

Relation between maximum number of teeth per half-row and width of radula, *Mexichromis porterae* (calculated regression line), *Mexichromis antonii*, and *Mexichromis tura*. Symbols as in Figure 23

ticulate, six to seven long denticles on the outer ones." The distal points on the teeth shafts are not bicuspid (in the sense defined by BERTSCH, 1977), but show the acuspid shape diagnostic of species belonging to *Mexichromis*.

Discussion:

Mexichromis porterae was named after Wilmatte Porter Cockerell. It is a distinctive species, still rarely reported even though its original description was over 75 years ago. It appears to be more common subtidally than intertidally; only one of the 10 specimens I examined was collected intertidally, and its known distribution in Santa Barbara County is limited to "subtidal to 60 feet" [18m] (SPHON & LANCE, 1968: 79).

Mexichromis tura (Marcus & Marcus, 1967), *comb. nov.*

(Figures 3-K, 22 F - G, 23 - 25, 61 - 64)

References and Synonymy:

- Chromodoris tura* MARCUS & MARCUS, 1967: 55-56; 53, figs. 59-61; plt. 1, fig. 3. KEEN, 1971: 822. SPHON, 1972b: 59. BERTSCH *et al.*, 1973: 292, 293. KEEN & COAN, 1975: 43.
Glossodoris tura (Marcus & Marcus). ABBOTT, 1974: 355, fig. 4244.
Thorunna tura (Marcus & Marcus). BERTSCH & FERREIRA, 1974: 344-345. BERTSCH, 1976b: 158

Material Examined and Distribution:

- 1) 1 specimen, La Paz area; *leg.* E. Janss, Jr., April 1974 (HB 435; LACM)
- 2) 3 specimens, intertidal, La Cruz, Nayarit, Mexico; *leg.* F. & R. Poorman, 3 January 1976 (HB 418 A-C; LA CM A 8477)

This species is very rare. It has been reported from one specimen collected at Deale Beach (Fort Kobbe Beach), Panama (type locality) and 4 specimens collected at Sayulita, Nayarit. The new material adds the southern

Gulf of California to its range. The species has a disjunct known distribution from 3 widely scattered localities in the Panamic province.

External Morphology and Coloration:

Center of dorsum is dark violet to nearly black, with reddish spots and dashes scattered throughout, and yellowish streaks around its border (MARCUS & MARCUS, 1967: plt. 1, fig. 3). Notum is surrounded by a broad bluish-white margin within which is a complete orange band around the animal. Foot dark violet with an orange midline on the dorso-posterior surface. The animal collected by E. Janss had yellow markings instead of the red or orange markings of the holotype.

Radula:

Meristic characters of the radula are in Table 12 and plotted in Figures 23 - 25. The 3 known radulae have 42 to 67 rows of teeth. No rachidian tooth. The lateral teeth (Figures 61 - 64) have an acuspid shape throughout the majority of the tooth rows. Additional drawings of the holotype's radular teeth (USNM 576266, F 809) are presented in Figure 22 F - G.

Table 12

Radular variation in *Mexichromis tura*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
6	—	—	—	42	31
418 C	0.921	0.372	1:2.48	67	—
435	0.703	0.404	1:1.74	57	41

⁶MARCUS & MARCUS, 1967.

Explanation of Figures 57 to 62

Scanning Electron Micrographs of the Radular Teeth of
Mexichromis tura and *Hypselodoris californiensis*

- Figure 57: *Mexichromis tura*; inner lateral teeth (HB 418 C) ×800
 Figure 58: *Mexichromis tura*; innermost lateral teeth (enlargement of Figure 57) (HB 418 C) ×2400
 Figure 59: *Mexichromis tura*; teeth from middle of half-row (HB 418 C) ×800

- Figure 60: *Mexichromis tura*; lateral teeth (HB 418 B) ×800
 Figure 61: *Hypselodoris californiensis*; overall view of several tooth rows (HB 252 B) ×200
 Figure 62: *Hypselodoris californiensis*; outermost lateral teeth (HB 252 B) ×675



Figure 57

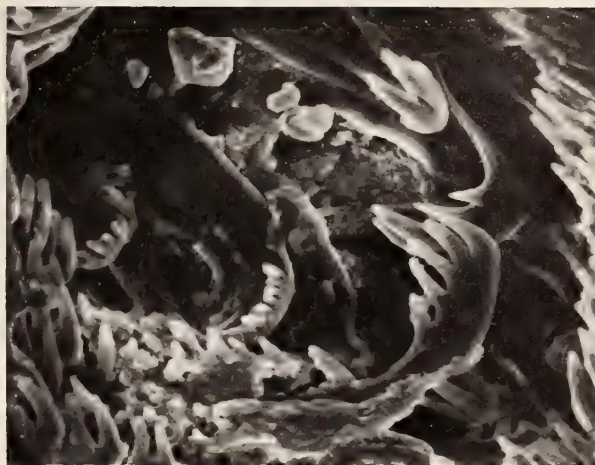


Figure 58



Figure 59



Figure 60



Figure 61



Figure 62

Discussion:

Examination of additional specimens has resulted in the re-evaluation of the generic placement of this species. In the original description, MARCUS & MARCUS (1967: 56) wrote, "The length of the first denticle behind the cusp makes the decision between *Chromodoris* and *Hypselodoris* difficult. One or two innermost teeth are not sufficient to define such a species generically. In *Chromodoris* most teeth are unicuspidate, hook-shaped and serrate on the outer side; in *Hypselodoris* most are bicuspidate or bifid." Placement of the species into *Mexichromis* more clearly differentiates between the Chromodoridinae. A glance at the scanning electron micrographs shows that the majority of teeth of *M. tura* are acuspidate. Such a total impression is biologically meaningful, since the morphological trait is present throughout an entire multi-structural functioning unit.

BERTSCH & FERREIRA (1974: 344-345) transferred this species to the genus *Thorunna* Bergh, 1877. This is inadequate, because even though the innermost lateral tooth is twice as broad as the following tooth, the gestalt pattern of *Thorunna* first lateral teeth is highly different from that of *Mexichromis tura*. Figures 57 and 58 of this work and fig. 61 of MARCUS & MARCUS (1967: 52) show an innermost tooth with a broad base (but with a greater basal length), that does not appreciably increase in width posteriorly. The 1st lateral tooth of *Thorunna* widens posteriorly, so that its greatest breadth at least equals the length of the tooth's base; and its base approaches a chevron-shape (cf. BERGH, 1878a: plt. 63, fig. 18; RISBEC, 1928: figs. 48-50; BABA, 1949: figs. 61-63; BURN, 1966: figs. 6 and 8; ER. MARCUS & EV. MARCUS, 1970: fig. 21). This shape does not occur in *Mexichromis tura*.

Discussion of *Mexichromis*

The distinctive radular morphology is probably indicative of a trophic specialization among the members of this genus. Although the members of the Chromodoridinae are rasping sponge feeders (cf., for instance, YOUNG, 1970), sharing basic radular structural similarities, there are a variety of teeth shapes that characterize each of the major generic evolutionary lineages within the subfamily. Detailed laboratory and field studies are needed to correlate feeding specificity with the different radular tooth patterns, similar to studies done on broader samplings of different opisthobranch taxa (BERTSCH, 1974; BLOOM, 1976).

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Reviews of Biology of Commercially Important Squids in Japanese and Adjacent Waters

I. *Symplectoteuthis oualaniensis* (Lesson)

BY

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(7 Text figures)

Symplectoteuthis oualaniensis^{*}, an oceanic squid of the family Ommastrephidae, is distributed in the vast warm waters in the Indo-Pacific region, but it has been commercially utilized only in Okinawa (Japan) and Taiwan (Republic of China). This species frequently has been encountered in such large numbers during oceanographic observations along warm water Japanese coasts (ITAKURA, 1977) that a large stock exists for fisheries exploitation. A report of the R/V *Shoyo-Maru* Expedition to the Gulf of Arabia described the existence of a large school of *S. oualaniensis* from the waters off Karachi, Pakistan (documented from Far Seas Fisheries Research Laboratory, 1976).

In spite of the economic importance of this squid, very little information on biology and fisheries is available. CLARKE (1966), YOUNG (1975) and WORMUTH (1976) briefly reviewed the biology of this species, while TUNG *et al.* (1973), TUNG (1975, 1976a, 1976b), Ryukyu Fisheries Experimental Station (1971) and Okinawa Prefectural Fisheries Experiment Station (1972) contributed a great deal of fishery-biological information of this interesting squid in the Northwest Pacific. This paper reviews chiefly these recent Chinese and Japanese contributions.

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IDENTITY

Symplectoteuthis oualaniensis (Lesson, 1830) is a species of relatively large animals among the family Ommastrephidae. The largest specimen reported by CLARKE (1966) was 30.5 cm ML (female), but individuals of this species grow much larger. Two females from the Indian Ocean measured 41 cm and 46 cm, respectively (Okutani, unpubl.).

This species is similar to the partly sympatric *Ommastrephes bartrami* (Lesueur, 1821) at a glance, but is easily distinguished from it by its fused mantle-funnel connective (on one or both sides) and an oval patch of photophores on the antero-dorsal surface of the mantle. CLARKE (1965, 1966) noted the existence of a smaller form within the *S. oualaniensis* population that has no photophores. YOUNG (1975) stated that the form with photophores will be considered to be true *S. oualaniensis*, not only for convenience's sake, but also because of its far more frequent occurrence. WORMUTH (1976) took the same view as Young and considered that the 2 forms likely are distinct species.

DISTRIBUTION

Rhynchoteuthion larvae of *Symplectoteuthis oualaniensis* may be contained among those reported as "*S. oualanien-*sis-type larvae" by OKUTANI (1964), OKUTANI & MCGOWAN (1969), SHOJIMA (1969) and YAMAMOTO & OKUTANI

^{*} English version of the proceedings of the symposium on the current status of cephalopod fishery in the waters around Japan, held at Niigata, Japan, 10-11 March 1977

^{*} ZUEV *et al.* (1975) incorrectly applied the generic name *Sthenoteuthis*

(1976). The "*S. oualaniensis*-type larvae" are characterized by: (1) a long "proboscis" (fused tentacles), (2) fewer mantle chromatophores than in *Todarodes pacificus* larvae, (3) smaller size in comparison to the equivalent stage of *T. pacificus* (i. e., the tentacles separate at a stage smaller than 7 mm ML), and (4) a pronounced intestinal photophore (CLARKE, 1966; Nesis, personal

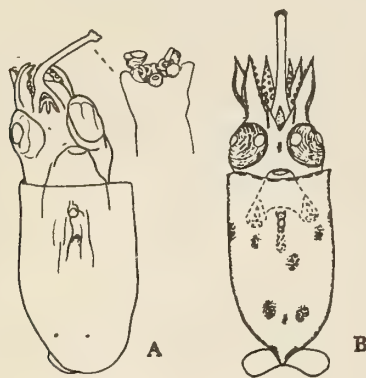


Figure 1

Rhynchoteuthion of *Symplectoteuthis oualaniensis*

A: After CLARKE (1966)

B: After NESIS (unpublished)

communication) (Figure 1). A large number of this rhynchoteuthion is distributed in the surface waters around Japan and Taiwan, but separation of true *S. oualaniensis* rhynchoteuthion from larvae of other sympatric ommastrephid species has not always been well established. Rhynchoteuthion larvae of *S. oualaniensis* may occur in summer in more offshore waters where those of *T. pacificus* are seldom distributed then. At a juvenile stage of ML 5 - 6 cm, *S. oualaniensis* is easily distinguished by the very pronounced intestinal photophore and the mantle-funnel fusion (the latter characteristic is not distinct in early larvae the integument of which is still very delicate). Juveniles frequently are aggregated in inshore waters of oceanic islands. According to the observations of one of us (T. O.), such aggregations of juveniles were found at Hachijo Island and Ogasawara (Bonin) Islands. Juveniles dip-netted near the Seychelles in the Indian Ocean (OKUTANI, 1970) and from Guadalupe Island, Mexico (Invertebrate Collection in the Scripps Institution of Oceanography) were also examined. YOUNG (1975) also recognized the abundance of juveniles in some insular areas by the evidence from birds' stomach contents. On the basis of an observation on behavior of a dip-netted juvenile that adhered to the bottom of a con-

tainer, Okinawa PFES (1972) assumed that the animal may crawl on the bottom in its natural environment. It is difficult to believe that this assumption was correct, as such behavior was most unlikely a normal posture.

Symplectoteuthis oualaniensis is known to be abundantly distributed in the surface waters both day and night, as it frequently is jigged or dip-netted at the surface and also is seen "flying" over the sea surface (ITAKURA, 1977). No direct evidence on vertical distribution of this species has been available. YOUNG (1975) inferred that this species may have a vertical distribution similar to that of the related genus, *Ommastrephes*, that is known to occur from the surface to depths of 1500 m.

The major fishing grounds are located on the southwestern coasts of Taiwan (TUNG, 1976a) and beyond the 200 m-contour off the Ryukyu chain (Ryukyu FES, 1971) (Figure 2). The fishing season near Taiwan is from March to November with the peak in May - August. Fishing is most productive at water temperatures above 26° C and particularly around 28° C. In the Ryukyu waters, the fishing season lasts from May to October at Yaeyama Region and from June to November at Okinawa Region. The surface water temperature for the season varies from 22° C to 28° C. The coastward shift of the 27° C-isotherm corresponds well to the location of the fishing grounds (Ryukyu FES, 1971). The landings of *Symplectoteuthis oualaniensis* at 2 major fishing ports in Taiwan and one in Okinawa are shown in Table 1. At 29° N, 135° E, this squid is continuously seen from May to October, particularly frequent at above 23° C in surface temperature at the station (ITAKURA, 1977).

Table 1

Landing of *Symplectoteuthis oualaniensis* in Taiwan (Kaohsiung and Hengchun) and in Okinawa (Itoman) (TUNG *et al.* 1973; Ryukyu Fisheries Experimental Station 1971). Unit: Kg

Year	Taiwan		Okinawa
	Kaohsiung	Hengchun	Itoman
1966	4	4	42014
1967	4	4	47659
1968	4	4	41501
1969	4	4	29907
1970	149556	6414	49166
1971	106566	3837	4
1972	28219	1181	4

⁴No published data are available.

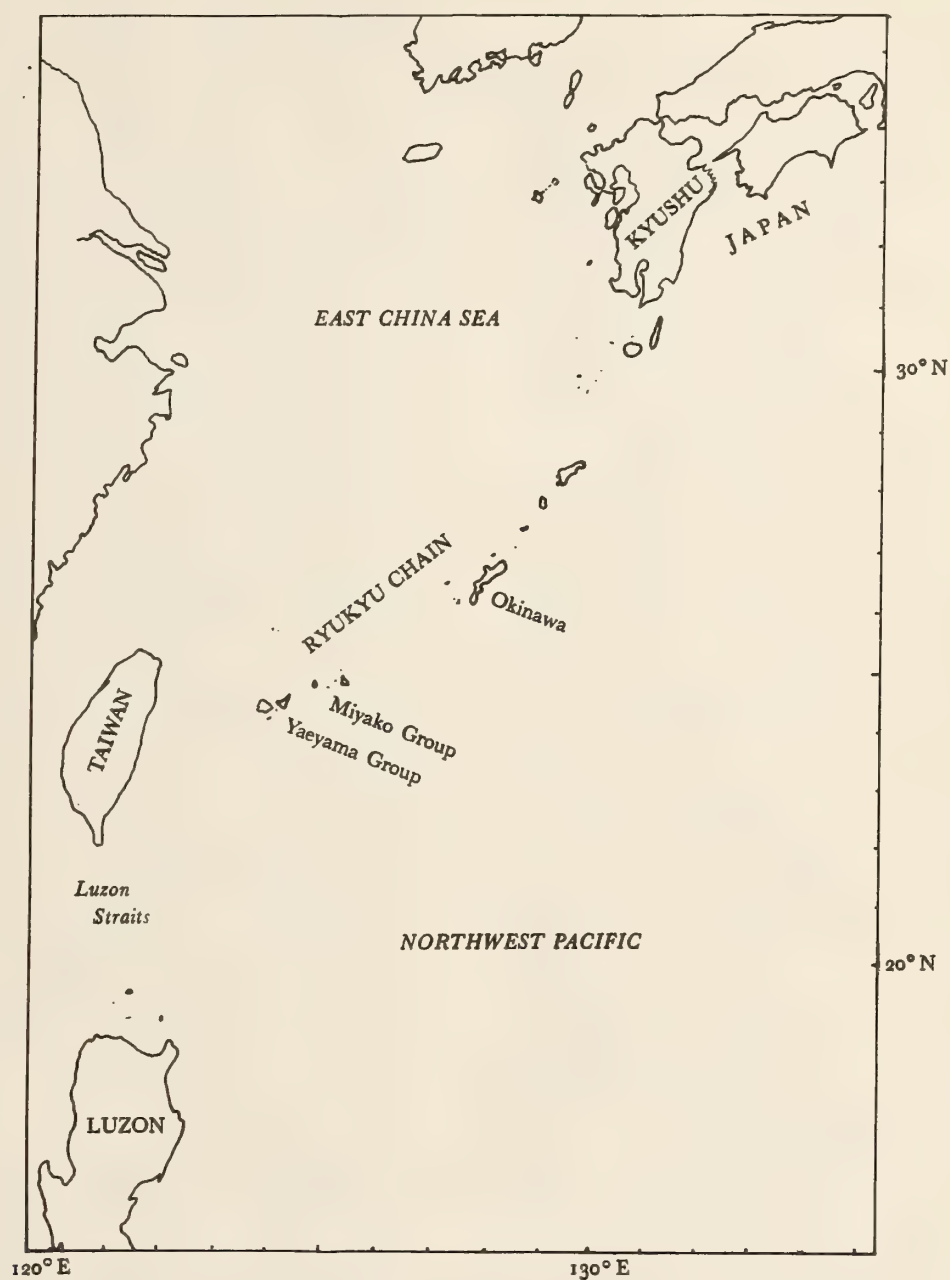


Figure 2

Index Map for Okinawa - Taiwan Area

GROWTH

TUNG *et al.* (1973) recognized 2 size groups³ in May: 12 - 18 cm ML and 19 - 24 cm ML. The smaller group grew to 16 - 22 cm in mid- to late June, while the larger group vanished from the fishing ground. Simultaneously another school with a mode at 12 - 13 cm ML entered the area and similar small-sized groups are recruited continuously until early September. Recruits grew as big as 16 to 17 cm by November (Figure 3). Therefore, the squid grows 4 cm in 2 months (from early May till early July and from early September till early November). Such a recruitment of smaller size groups has also been apparent in the sea around Okinawa (Ryukyu FES 1971 and Okinawa PFES 1972). The relation between ML and body weight (BW) given by TUNG *et al.* (1973) is:

$$\log BW = 2.8481 \log ML - 4.0088.$$

According to the most recent study by NESIS (1977), the population of *Symplectoteuthis oualaniensis* in the western tropical Pacific is composed of 2 different groups, namely, a small and early-maturing group (EM) and a large and late-maturing group (LM). The EM matures at 10 cm ML in males and 13 cm ML in females with a life span of about 8 - 9 months, while the LM matures at 12 - 13 cm ML in males and 20 - 24 cm ML in females with a life span slightly longer than one year. The EM is distributed only in the central part (between 55° E and 175° W, and 10° - 15° N and S) of the whole range of the species. The EM differs from the LM in the absence of the dorsal photophore patch, which is differentiated in the LM at about 10 cm ML. Nesis also mentions that spermatophore and heterocotylus are different from each other. This supports the view of CLARKE (1966) and WORMUTH (1976) that 2 forms within *S. oualaniensis* are different from each other not only in the presence (and absence) of the dorsal light organ but also in size at maturity, maximum size, abundance and distributional range. Nesis thinks that these groups are genetically differentiated "superpopulations" within the species.

REPRODUCTION

The left arm IV is hectocotylyzed and is developed from about 11 cm ML onward. Unlike that in *Todarodes pacificus*, in which the distal half of the right arm IV is modified into comb-like papillae mostly with suckers, the distal half (50.3 ± 2.66%) of the hectocotylyzed arm completely

lacks suckers and has a sharp fleshy ridge with smooth or undulated sides. The hectocotylyzed arm is slightly longer (114.9 ± 5.8%) than the normal right arm IV.

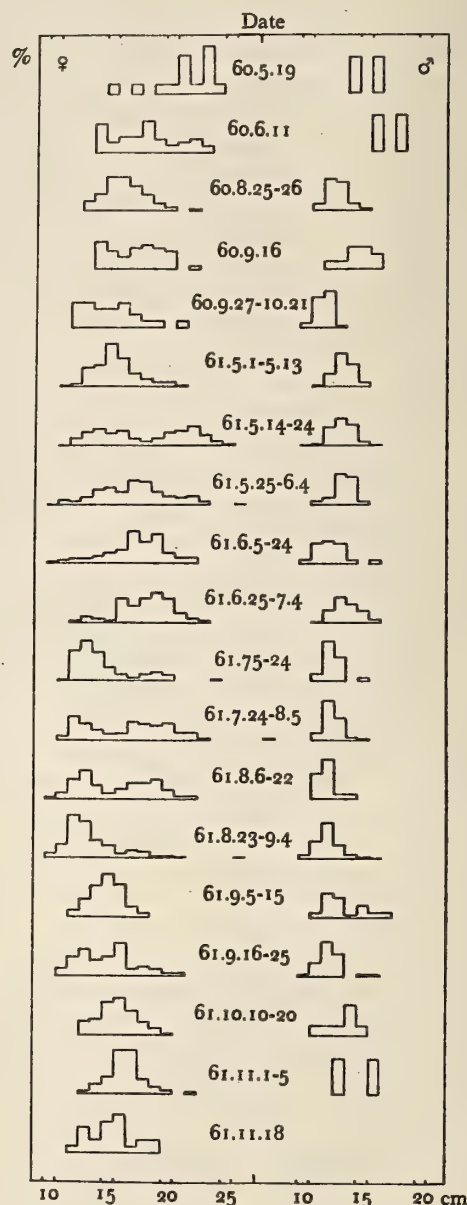


Figure 3

Seasonal Change of Mantle Length Composition
(TUNG *et al.*, 1973)

The years 60 and 61 correspond to 1971 and 1972 A. D.

³ On photophore-bearing type only

Concerning the sex ratio of this squid, TUNG *et al.* (1973) and TUNG (1976a) found that the males comprise about 31% of the population in the early fishing season and 21% in the closing season (average 25%). The sex ratio is 1:1 at the stage of 10-13 cm ML, while males gradually diminish in numbers after 14 cm ML. Females strongly predominate in the commercial catches in Okinawa, comprising some 70-80% thereof (Okinawa PFES, 1972). This may coincide with the fact that males mature much earlier than females and disappear from the fishing grounds. Also, schools appear first in the north of Luzon with a high ratio of males and migrate northward along the Kuroshio Current, spreading to the southwest and east of Taiwan and then northward to the Ryukyu Region.

TUNG (1976a) observed copulating behavior at 0300 on June 28, 1973, at surface at 21°06'N; 120°58'E, north of Luzon. The observed pair was a male about 13 cm and a female about 20 cm. The female which had been swimming about 20 cm ahead of the male suddenly changed its orientation and grasped the male in a head-to-head position. The male then changed its position to form an angle of 45° with the female, but soon returned to the linear head-to-head position while sinking out of sight.

Among 37 males captured at that time, 35 carried spermatophores and among 136 females, 72 were impregnated with spermbulbs. This species does not seem to eject all spermbulbs at one copulation but may copulate with several females. Artificial fertilization experiments were made on board the ship at the same time. Among 3 trials, the most successful one had a fertilized egg develop until blastopore formation and differentiation of the eyes.

The asymmetrical ripe eggs are translocated to the oviduct when the ova are 0.75 mm in major diameter. The number of ova rapidly increases since at 15 cm ML, 5 g of ovary contain 10 000 to 20 000 eggs. The relation between ovary weight (W_{ov}) and ML is:

$$W_{ov} = 4.18 \text{ ML} - 65.34$$

The largest ovary ever measured was 58.4 g and contained 250 000 eggs.

Eggs in the oviduct measure 0.788 ± 0.03 mm ($0.714 - 0.872$ mm) in major diameter. The minor diameter is about $84.54 \pm 1.95\%$ ($80.03 - 87.86\%$) of the major diameter. The maximum weight of the oviduct is about 40% of the entire female reproductive system. The eggs in the oviduct attained a maximum weight of 33.1 g, in which there were 123 562 eggs present.

Nidamental glands are as small as 2 cm in squid of 15-16 cm ML but grow to 7 cm at 18-19 cm ML. The relation between the length of the nidamental gland (Ln) and mantle length shows a logarithmic curve in which the point of inflexion is present at 17.2 cm ML or 4.7 cm in



Figure 4

$$GLI = (Ln/ML \times 10^2) \text{ (TUNG, 1976a)}$$

Ln (Figure 4). The relation between weight (W_n) and length of the nidamental gland is:

$$W_n = 0.070924 \text{ Ln}^{2.335954}$$

The relations among various measurements in the male reproductive system and ML are shown in Table 2 (TUNG, 1976a).

The spermbulbs are implanted around the female's mouth. Close examination of 10 females showed 15.2 spermbulbs implanted on the ventral side of the inner lip of the buccal mass, 6.1 on the dorsal side, 0.2 on the outer lip, 0.3 on the inner surface of the buccal membrane, 1.4 in the outer region of the same, and 0.6 on other places, such as the base of the arms. The spermbulbs planted usually are covered by a gelatinous covering and are embedded in the soft tissues of the lips for $\frac{1}{3} - \frac{2}{3}$ of the length of the bulbs. All of the females larger than 24 cm ML are implanted with spermbulbs, ranging from 1 to 83 bulbs (Figure 5). The seminal receptacle usually is composed of 2 vesicles, but occasionally of 5-6. They are unevenly distributed around the buccal membrane and vary from 9 to 163 in number. The seminal receptacles are usually undeveloped in females smaller than 13 cm ML. The ratio of specimens having receptacles exceeds 50% at 15 cm ML and reaches 100% at 18 cm ML.

Table 2

Relation between measurements in male genital organ and ML (TUNG 1976 a).

Entry	Corr. Coef.	Regression formulae
Testis weight — ML	0.865**	$W_t = 0.0364ML - 2.836$
Seminal duct w. — ML	0.792**	$W_{vd} = 0.0673ML - 6.519$
Seminal duct w. — Testis w.	0.798**	$W_{vd} = 1.542W_t - 0.666$
Seminal duct l. — ML	0.357**	$L_{vd} = 0.3612ML + 15.881$
No. of spermatophore — ML	0.497**	$N_{sp} = 0.9846ML - 99.38$
No. of spermatophore — Testis w.	0.255*	$N_{sp} = 11.680W_t + 7.993$
No. of spermatophore — Seminal duct w.	0.718**	$N_{sp} = 17.085W_{vd} - 9.185$
Spermatophore l. — ML	0.703**	$L_{sp} = 0.1349ML + 0.503$

*Significant level at 5%, ** at 1%, respectively.

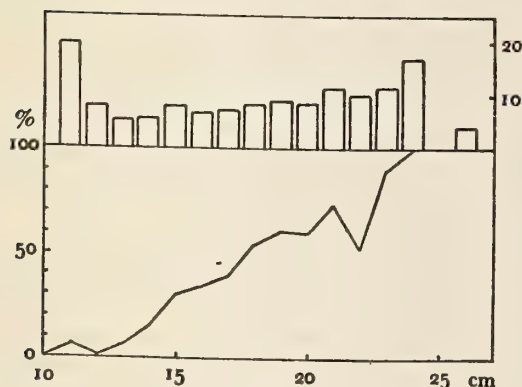


Figure 5

Ratio of Impregnation of Sperm Bulbs on Females (lower panel) and Average Number of Sperm Bulbs (upper panel) by Mantle Length (TUNG, 1976a)

TUNG (1976a) defined 3 stages of maturity: "immature" for less than $L_n = 2.5$ cm or 15.5 cm ML, and "fully mature" for L_n over 7.5 cm or ML over 19 cm. The stage between these two may be "mature." Among "immature" specimens, W_n 1 g are allocated as "mature," and those in which GW/BW exceeds 10% are allocated as "fully mature" (Figure 6) (GW = gonad weight; BW = body weight).

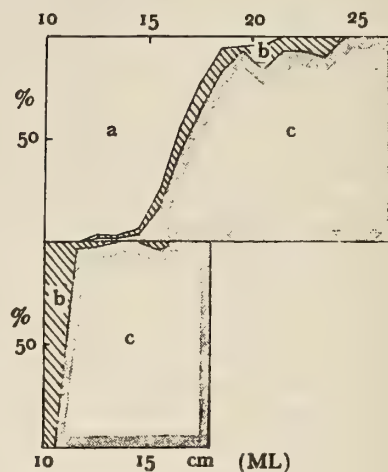


Figure 6

Ratio of Three Grades of Maturity by ML Classes (TUNG, 1976a)

Female (upper panel), a: immature ($W_{ov} < 3$ g), b: mature ($W_{ov} > 3$ g), c: fully mature (ova present in oviduct)
Male (lower panel), b: mature (Wt. 2 g), c: fully mature (spermatophores present)

At the time of the first appearance of the squid schools in the southwestern waters off Taiwan, most of the females are immature. They gradually become mature and spawn in June. Along with the disappearance of the large-sized squid, another population of small squid appears in July-August and they become fully mature in September-October. The third population that appears in November seems to mature in February-March of the next year. Therefore, the successive appearance of immature squids that mature several months apart well corresponds to the size composition. In conclusion, the *Symplectoteuthis oualaniensis* population in Taiwanese waters is composed of 3 different (seasonal) subpopulations.

Among the population that appears in the north of Luzon, some fully mature females are found. The schools that appear in the southwestern waters off Taiwan in June are composed of squids of advanced maturity. This school may spread in a clockwise direction but partially migrate up north to the Miyako Islands via the East of Taiwan. The mature individuals move ahead of the less mature squids. Spawning of these squids in the South China Sea is corroborated by SHOJIMA (1970) who reported rhynchoteuthion larvae which probably belong to

this species, of 0.6 - 6.4 mm in summer. Rhynchoteuthi-
ons of *Todarodes pacificus* never occur there in that season.

FOOD

TUNG *et al.* (1973) and TUNG (1976b) found the maximum content of a stomach to be 52.6 g (at 27 cm ML), but the contents usually weigh 1 - 3 g. Empty (less than 0.5% of body weight), medium (less than 3%) and full (over 3%) stomachs occupy 62%, 33% and 4%, respectively, of examined stomachs. The relation between ML and weight of a full stomach (W_s) is:

$$\log W_s = 3.4576 \log ML - 6.751$$

According to this, the average full stomach contents of the squid between 10 and 25 cm ML is 3.24 to 5.25 (Figure 7).

The stomach contents are composed of pieces of squid flesh, horny rings, hooks, squid eyeballs, jaw plates, fragments of gladii, scales of fishes (probably 4 - 5 cm in body length), vertebrae, fish eyeballs, crustacean remains, spermbulbs and parasites. The squids that preyed mainly on fish accounted for 36.7% (among them $\frac{2}{3}$ preyed entirely on fish), on crustaceans - 20.5%, on squids - 18.4%

and on unidentified substances - 9.8% of examined squid specimens.

A regional tendency exists in prey-species composition: squid captured in the southwest of Taiwan contained mostly fish, in the east of Taiwan, a mixture of fish and squid, and around Okinawa more frequently crustaceans. Seasonal differences may be within the range of areal variation.

The stomach content index ($= SW/BW \times 100$) is higher in the early half of night (maximum 1.43) and lowers towards dawn. The relation between maturity and food intake is not clear, but the larger the squid grows, the smaller the index becomes.

YOUNG (1975) stated that *Symplectoteuthis oualaniensis* mainly preys upon fish. He reports that a single stomach contained remnants of 14 fishes. Other prey were enoploteuthid squids and various crustaceans, but the latter were thought to be from the ingested fish stomachs. WORMUTH (1976) listed 15 fish species that were identified from otoliths: *Stolephorus purpureus*, *Exocoetus volitans*, *Oxyporhamphus micropterus*, *Ceratoscopelus*, *Centrobrunchus*, *Vinciguera*, 2 species each of *Hygophum*, *Diaphus*, and *Myctophum*, and species of *Centrolophidae*, *Gempylidae* and *Holocentridae*, all in Hawaiian waters. Besides squid beaks, he identified *Hyaloteuthis pelagica*, *Onychoteuthis banksii* and an enoploteuthid squid in the diet of *S. oualaniensis*. His description on a way of preying upon myctophids based on his observations on board ship is quite similar to what we have observed.

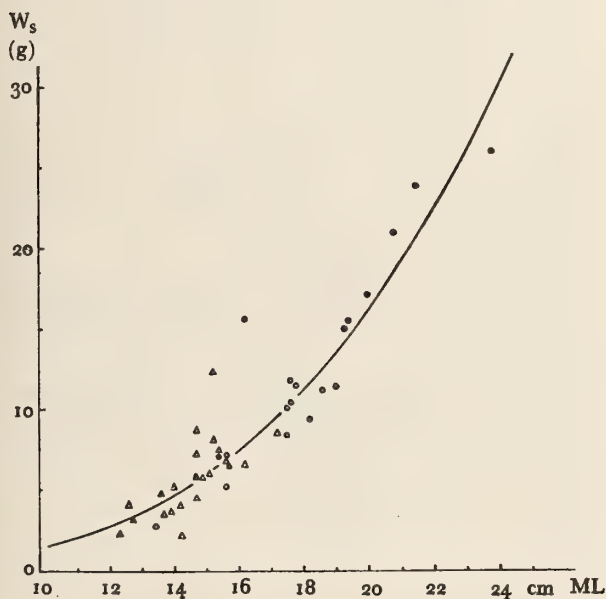


Figure 7

Relation between Content Weight of full Stomach (W_s) and Mantle Length (TUNG, 1976b). Dots: fully mature; circles: mature; triangles: immature specimens

PREDATORS

No report has been available on predators of this squid in the Northwest Pacific, except a finding of *Symplectoteuthis oualaniensis* in the stomach content vomited by an unidentified sea bird (T. O.).

CLARKE (1966), YOUNG (1975), and WORMUTH (1976) listed as predators of *Symplectoteuthis* the sea birds: *Phaeton rubricauda*, *Puffinus nativitatis*, *Pterodroma alba*, *Sterna fuscata*, *Anous stolidus*, *A. tenuirostris*, *A. minutus*, *Gygis alba*, *Porcelsterna caerulea*, *Sula piscator*, *S. sula* and *S. sp.* As fish predators, *Coryphaena hippurus*, *Gempylus aerpens* and several tuna are listed by WORMUTH (*op. cit.*).

PARASITES

TUNG (1976a) found that 13.2% of females and 6.0% of males examined were infested by parasites, of which 92.6% were trematodes 0.6 - 6.0 mm long. The rate of in-

festation is higher in the population in the southwest-south of Taiwan, lower in the east of Taiwan, and lowest in Okinawan waters. In general, the larger the squid, the higher the rate of infestation: 7.0% for immature, 15.5% for mature, and 34.8% for fully mature (average 13.2%).

FISHING

Symplectoteuthis oualaniensis has been commercially utilized only in Taiwan and Okinawa. The traditional fishing boat in Okinawa is a small row-boat of less than 1 ton. The annual squid and cuttlefish landings during 1947 to 1969 was 325 tons, and 70% was *S. oualaniensis* (Ryukyu FES, 1971). Motor-driven squid jigging machines have been used experimentally and the results revealed that the machines catch slightly smaller squids (Ryukyu FES, 1971).

Symplectoteuthis oualaniensis is a byproduct in the Taiwanese fishery. TUNG *et al.* (1973) found that *S. oualaniensis* seldom stayed near the boat during experimental use of motor-driven jigging machines, even if they showed positive phototaxis to the fishing lights. The squid in the shadow of the boat are more easily attracted by jigs operated by machine, but those that stay in dim light at 15 - 25 m depth are more accessible to hand lines. Poor catches are obtained during full moon.

Another technical problem is that the arms of *Symplectoteuthis oualaniensis* are easily broken by motor-driven jiggers (originally designed for *Todarodes pacificus*); *e.g.*, while 499 squids were captured, 365 broken arms (without whole animal) were hooked. This means almost half of the hooked squids were not taken aboard.

The size of squid caught in Taiwan and Okinawa is good for bait for the tuna long line fishery. *Symplectoteuthis oualaniensis* also is good for human consumption and is being used on a small scale. However, attracting and keeping the schools under the fishing light for long duration and preventing broken arms are technical problems to be overcome.

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Possible Predation on *Nautilus pompilius*

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(1 Plate; 1 Text figure)

INTRODUCTION

THE MORE RECENT REVIEWS of the natural history of *Nautilus pompilius* Linnaeus, 1758 (MILLER, 1947; SHIMANSKY, 1962; STENZEL, 1964) make little mention of predators or predation. WILLEY (1902) reported seeing *Nautilus* specimens in which the hood had been bitten and attributed this to possible attacks by fish, sharks or conger eels and nuptial combats. More recently, HAVEN (1972) reported fighting between young and adult males of *N. pompilius*; however, this report could also be interpreted as attempted cannibalism.

As far as we can determine, no analytical studies have been done on the possible extent of predation on *Nautilus pompilius*. While the present paper was being reviewed after submission for publication, FAULKNER (1977) mentions the existence of boreholes in living *Nautilus* from New Caledonia. Although he suggests that octopus were the possible borers, he provides no detailed analysis or description of the boreholes. In the present paper, we analyze boreholes found in numerous specimens of *N. pompilius* and suggest that some boring organism is an important predator on *Nautilus*. We also describe the borings and responses observed, consider the identity of the boring organism, and analyze the pattern of boreholes and the possible frequency of predation on *N. pompilius* by these organisms.

MATERIAL AND METHODS

Except where noted, all *Nautilus pompilius* examined in this study were purchased as empty shells from commer-

cial sources within the last 3 years. All were imported by Filipino suppliers and were presumably collected in the vicinity of the Philippine Islands. We do not know if the shells contained animals when they were collected. Specimens examined include: Harvard University, Museum of Comparative Zoology: *N. pompilius*, MCZ 184601, 142-510, and 2 uncatalogued specimens; *N. repertus*, MCZ 211689; University of Iowa: *N. macromphalus*, SUI 40081 - 40093; *N. scrobiculatus*, SUI 623; *N. pompilius*, SUI 1090, 1092, 40045 - 40079, 40096 - 40100, 42469 - 42477; and *N. cf. N. repertus*, SUI 40094 - 40095. Measurements of borehole outer diameter (greatest dimension) and shell parameters were made with vernier calipers. The diameter of the shell was measured at the borehole. Diameters of the largest shells were measured with a millimeter rule. Terminology follows CARRIKER & YOCHELSON (1968).

RESULTS

We examined 150 shells of *Nautilus pompilius*; 43 (28.7%) of them were found to be bored. Boreholes were also observed in other species of *Nautilus*: the frequencies of borings were 1 of 13 *N. macromphalus*, 3 of 3 *N. repertus* and 1 of 1 *N. scrobiculatus*. The sample sizes for these species are too small for analysis and the remainder of the paper will be concerned with *N. pompilius*. A smaller percentage (24%) of juvenile shells (those without a black lining on the inner edge of the aperture) than adults (79%) had boreholes, but the sample size of adults ($n = 15$) is smaller than that of juveniles ($n = 135$). The virtual absence of bored shells in the range of 60 - 110 mm

diameter is due to our lack of specimens in that size range. A total of 11 specimens (6 adults and 5 juveniles) had more than one borehole. The frequency (50%) of adults with multiple borings is higher than the frequency (16%) of multiply bored juveniles ($X^2 = 21.8$, 1 df, $p < 0.005$). The largest number of complete boreholes observed on any single specimen was 4.

Boreholes are regularly situated relative to the height of the whorl. Only 4 of 60 boreholes were in the lower lateral and umbilical lateral regions of the shell. The mean position of the boreholes was at $\frac{3}{4}$ the distance from the umbilical shoulders to the venter (*i. e.*, generally in the ventrolateral region of the body chamber).

The outer diameters of the boreholes are significantly related to the diameters of the shells at the borings ($r = 0.76$, $p = 0.001$). Regression lines ($Y = 0.012 X + 0.93$;

$X = 48.63 Y - 16.53$) computed from the data in Figure 7 are significantly different from 0 at the 95% confidence level. If incomplete boreholes are included in the calculations, the equations ($Y = 0.011 X + 0.89$; $X = 44.90 Y - 1.72$) still do not contain 0. The r value is reduced to 0.70, but is still significant ($p < 0.001$).

The outer openings of the boreholes are irregular in outline ranging from circular to nearly cruciform. However, they all appear to be variations on a basic plan. At the inception of boring, the outer opening is almost circular. As boring proceeded, the circular outer hole developed a variably shaped elongation in what appears to be a random orientation. Incomplete boreholes have a bossed bottom. The height of the boss is smaller in incomplete holes that deeply penetrate the nacreous layer than in shallower holes (Figure 5). The final borehole shape is a circular outer opening with 2 chamfers opposite each other that extend beyond the countersunk edge of the borehole (Figure 4). Incomplete holes that penetrate deeply into the nacreous layer of the shell appear to be more irregular than those not reaching it. The interior openings of the completed borings range from circular to elliptical (Figure 6). No correlation between the shapes of the inner and outer openings was noted. Shelves were present in most completed borings. Borehole longitudinal sections vary from truncated circular to irregularly conical to truncated spherical parabolic boreholes. Many boreholes were countersunk as well.

The intensity of the reaction of *Nautilus pompilius* to borings varied from none to extreme (Figure 1); 13 specimens showed evidence of a response. Most reactions were confined to the formation of a small black discoloration around the interior opening of the borehole. The possibility that this was produced by the boring organism cannot be ruled out. One specimen (Figure 1) formed massive blister-like pearls of what is probably calcium carbonate together with black organic matter over the interior opening of one borehole and a thick black layer with a thin calcium carbonate layer around a second borehole. This latter borehole is not plugged, whereas the former appears to be completely plugged.

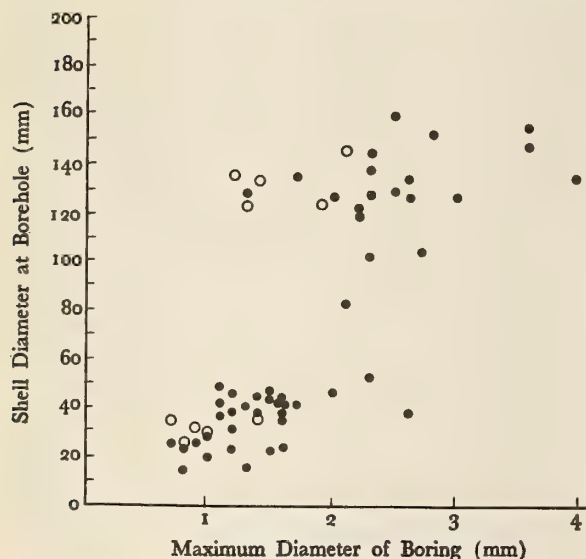


Figure 7

Scattergram showing the distribution of maximum borehole diameter compared to the conch diameter at the borehole. Open circles represent incomplete borings; closed circles represent complete borings

Explanation of Figures 1 to 6

Figure 1: Internal view of *Nautilus pompilius* with blister-like organic and calcium carbonate deposits around boreholes (SUI 40039) $\times 1$

Figure 2: External view of the specimen shown in Figure 1 showing the positions of the boreholes (SUI 40039) $\times 1$

Figure 3: *Nautilus pompilius* showing boring at about 160° of arc from the estimated position of the neponic constriction (SUI 40044) about $\times 2.1$

Figure 4: Initially circular boring with slit-like internal opening (SUI 40042; whitened with NH_4Cl) $\times 5$

Figure 5: An unfinished boring with a bossed bottom from the right side of the specimen shown in Figures 1 and 2 (SUI 40039; whitened with NH_4Cl) $\times 5$

Figure 6: Oval shaped boring on the right side of the specimen shown in Figures 1 and 2 (SUI 40039; whitened with NH_4Cl) $\times 5$



Figure 1

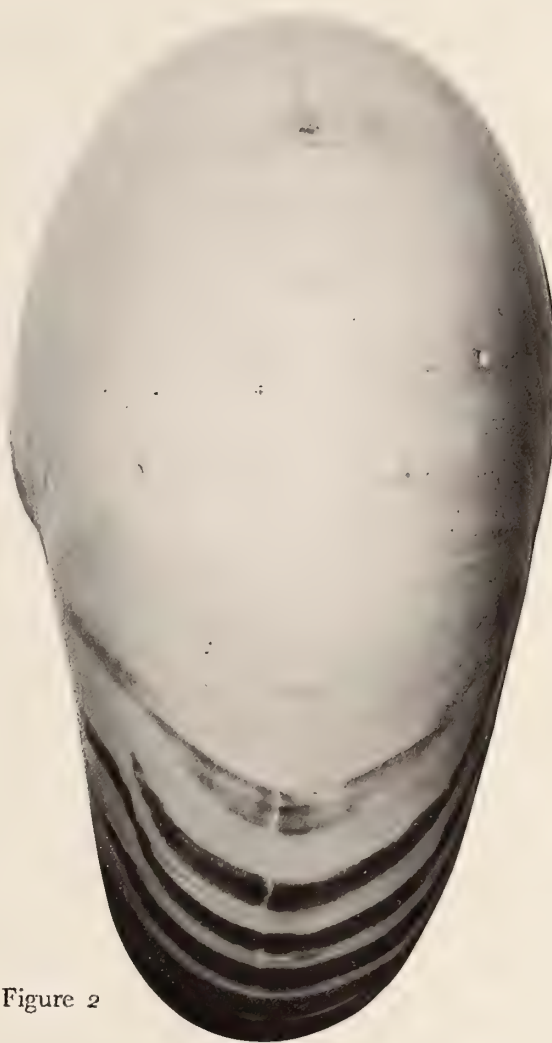


Figure 2



Figure 3

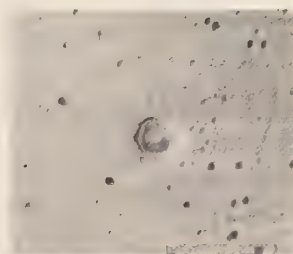


Figure 5

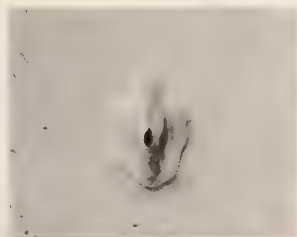


Figure 4



Figure 6

DISCUSSION

CARRIKER & YOCHELSON (1968) reviewed what was then known of predatory boring organisms which included turbellarians, coleoid cephalopods and gastropods. Turbellarians produce boreholes that are much smaller (0.15×0.19 mm) than any of those observed in *Nautilus pompilius* (CARRIKER & YOCHELSON, *op. cit.*). Coleoid borings are also generally smaller but some are large (2×3 mm) and vary from irregularly oval to cruciform in shape (PILSON & TAYLOR, 1961; WODINSKY, 1969, 1973; ARNOLD & ARNOLD, 1969). Some coleoid borings are at least superficially similar in gross shape to the borings we observed in *N. pompilius*. R. T. Paine (personal communication, 1 December 1976) from examination of our photographs stated that the borings shown in Figure 4 could certainly be due to *Octopus*. However, certain details of the structural features argue against this. Coleoid borings have not been reported to show double chamfers or countersinking which are characteristic of the borings that we observed. Coleoid borings are also highly variable in angle of penetration (ARNOLD & ARNOLD, *op. cit.*), whereas the borings that we observed are much less variable. The inner opening is usually at the center of the outer opening and in no case did we observe instances where the point of penetration was not at the extremity of the boring which commonly occurs in coleoid borings (ARNOLD & ARNOLD, *op. cit.*). Despite these differences the boring habits of Indo-Pacific coleoids have not been studied in detail, and therefore, a coleoid could be responsible for the borings.

Marine predatory boring gastropods include snails in the families Naticidae, Muricidae, Capulidae and Cymatiidae (CARRIKER & YOCHELSON, 1968). Capulids bore ciliary feeding bivalves. Cymatiid borings are neither well documented nor well known, but naticids and muricids are well known for their boring of other mollusks (CARRIKER & YOCHELSON, *op. cit.*). Prior to this report these two families have been thought to prey only on gastropods and pelecypods. While we know of no actual observations of snails boring *Nautilus*, the boreholes we report most closely resemble those made by predatory snails on other mollusks. While the generic and specific identity of the predator cannot be determined, the morphology of the boreholes suggests that a naticid predator would be more likely to be responsible than a muricid. The formation of bossed bottoms is characteristic of naticids (CARRIKER & YOCHELSON, *op. cit.*). One borehole (Figure 5) closely resembles an incomplete hole of *Polinices duplicatus* figured by CARRIKER & YOCHELSON (*op. cit.*: pl. 2, fig. 6). The boreholes in *Nautilus* differ from boreholes of other

naticids that have been studied in that they are not regularly circular. Even so, they all seem to have been initially circular and then to have become more irregular as boring proceeded. The possibility that the irregular boreholes in *Nautilus* were made by naticids is not necessarily unlikely because the prey species and borehole morphology of the Indo-Pacific naticid species are poorly known. Also the internal structure of the nautiloid shell is different from that of other mollusks and this may influence the final shape of the borehole. Similar variation in borehole morphology dependent on prey type was reported by CARRIKER & YOCHELSON (*op. cit.*).

The overall position of the majority of the boreholes in the ventrolateral region of the body chamber indicates a preferential positioning of the boring. The most likely reason may be that the predator preferred to attack the ventrally located soft parts (gonads, kidney and heart) of the nautilid rather than the retractor muscles or the organs of the dorsal portion of the mantle spaces in the umbilical lateral regions of the body chamber. If either a gastropod or a coleoid tried to bore in a more oral position, the *Nautilus* might be able to dislodge it by using one or more tentacles. This could explain why most borings are in the adapical half of the body chamber.

More *Nautilus pompilius* specimens were bored in the body chamber than in the phragmocone. Of 60 borings, only 12 completed borings are located in the phragmocone. It is not possible to determine if bored phragmocones represent attempted predation when the nautilid was living in that part of the shell or whether the boring was originally made into the phragmocone. Limited analysis of phragmocone borings was attempted because 5 of the 12 completed phragmocone borings appear to be plugged from the inside. When 2 (both juveniles) of these specimens were longitudinally sectioned, the internal opening of the borehole showed no appreciable reaction except for the plug the nature of which is unknown. However, the lack of reaction is not remarkable because the majority of the borings into the body chamber of juveniles show no reaction either.

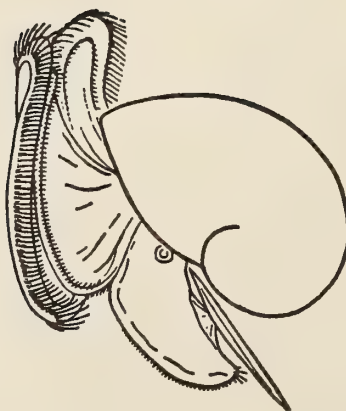
Attacks on *Nautilus* by predatory boring organisms have not been reported previously. Although we observed no actual attacks, the regular positioning of the borings, the existence of specimens showing reactions to the borings, and the high frequency of bored shells strongly suggest that *N. pompilius* is attacked by a predatory boring organism, most probably some species of coleoid cephalopod or naticid gastropod. Closer surveillance of traps in the future may lead to the identity of the predator. Field workers should be particularly watchful for species of naticids and coleoids associated with freshly bored nautilids.

ACKNOWLEDGMENTS

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Laboratory Culture, Metamorphosis and Development of *Aplysia brasiliana* Rang, 1828

(Gastropoda : Opisthobranchia)

BY

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(1 Text figure)

INTRODUCTION

BECAUSE OF THEIR increasingly important use in neurophysiological and behavioral studies (KANDEL, 1976) select species of opisthobranch mollusks have recently become the subjects of expanded field and laboratory culture studies (for review, see THOMPSON, 1976 and SWITZER-DUNLAP & HADFIELD, 1977). Laboratory culture techniques have been established for *Aplysia californica* Cooper, 1863 (KRIEGSTEIN, CASTELLUCCI & KANDEL, 1974) and *A. juliana* Quoy & Gaimard, 1832 and *A. dactylomela* Rang, 1828 (SWITZER-DUNLAP & HADFIELD, *op. cit.*). KRIEGSTEIN (1977) presents detailed descriptions of development in *A. californica*. Due to its geographical location, this laboratory has greatly expanded its interest (BLANKENSHIP & COGGESHALL, 1976) in the study of *A. brasiliana* Rang, 1828. This species is common to the South Texas Coast (STRENGTH & BLANKENSHIP, 1977) and adults are easily maintained in the laboratory. The results of this study provide simple culture techniques along with descriptions of metamorphosis and post-larval development of this scientifically useful marine gastropod.

METHODS

Natural sea water is used in the culture of veligers and post-metamorphic juveniles. This is collected, adjusted to 30 ppt., filtered through a 0.2 μ m membrane filter, and stored in carboys until ready for use. Living specimens of *Aplysia brasiliana* were collected from South Texas and maintained in the laboratory in artificial sea water of 28 to 30 ppt. at 18° C to 22° C. They were fed daily on a diet of "Laver" (commercial name of dried *Porphyra*). Eggs

laid by laboratory-held specimens of *A. brasiliana* hatch in about 8 to 10 days.

Prior to hatching, eggs are removed from the holding tanks and placed in open petri dishes containing natural sea water. This facilitates examination by microscope and provides a concentrated source of veligers following hatching. Water in the petri dish is changed daily until hatching. Preparation dishes (Pyrex No. 3250, 100×80mm) are used for the culture of the free-swimming veligers during the remainder of their larval development. Several weeks prior to their use as containers in the culture process, preparation dishes must be readied, or conditioned, for acceptance of veligers. This process involves the adding of 300 mL of paper-filtered natural sea water to each dish, replacing the cover and placing it in the laboratory where it receives normal room light. This procedure facilitates growth of a coating of diatoms or algae, or both, on the inner surface of the dish. Prior to the transfer of veligers, the preparation dish is emptied of old water, flushed a couple of times with filtered sea water, and filled with 300 mL of freshly aerated membrane-filtered sea water. Care is taken to prevent removal of the coating on the inner surface of the preparation dish. Fifty to 150 free-swimming veligers are transferred by means of glass pipettes into the preparation dish which is placed within 5 to 10 cm of a fluorescent lamp. Optimal results were obtained with light entering from the side of the culture containers. Cultures are maintained at temperatures of 21° C to 25° C and glass tops are retained on the preparation dishes at all times except for feeding or removing specimens for examination.

Feeding is accomplished by the addition of the unicellular algae *Isochrysis galbana* to the culture. Unialgal cultures of this species are maintained at peak or near-peak growth of 1 to 2 million cells per milliliter (PROVASOLI, 1968). Prior to feeding, 200 mL of *Isochrysis* culture

is centrifuged at 3800 rpm for 15 minutes. Following centrifugation, the supernatant culture medium is poured off and the concentrated "pellets" of *Isochrysis* cells are resuspended in 100 mL of aerated filtered sea water. This is allowed to stand in 2 centrifuge tubes for 24 hours prior to feeding. Once prepared, these tubes can be used for feeding for up to 3 days. One mL is pipetted from the surface region of this prepared medium and evenly distributed throughout the veliger culture. This gives an approximate density of 5 000 to 10 000 *Isochrysis* cells per milliliter in the culture medium. During feeding the culture water is vigorously mixed by use of the pipette. Feeding and mixing is done once daily.

Once initiated, the veliger culture requires little maintenance other than daily feeding and mixing. Cultures have been maintained for up to 70 days without water change. Survival rates by use of this method may vary, but can be easily maintained near the 50% level with minimal care. Two major sources of mortality account for this reduced survival rate. The veliger larva is pelagic in its natural environment and lack of stimulation by flowing current in this culture method apparently results in a settling out of moderate numbers of veligers during the first 7 to 10 days following culture initiation. These become trapped in the substrate, cease natural feeding activities, and eventually perish. The air-water interface accounts for the other major source of veliger mortality. Once a fast swimming veliger comes in contact with the interface, it becomes trapped on the water surface. Loss of veligers at the interface appears directly related to the density of veligers in culture; proportionally greater losses occur in crowded cultures. This problem is somewhat reduced by maintaining the water depth at approximately 5 cm. In addition, loss of veligers at the air-water interface can be minimized by routine daily examination beneath a dissecting microscope during which time trapped veligers may be resubmerged by dropping water from a pipette. The use of compounds (HURST, 1967; SWITZER-DUNLAP & HADFIELD, 1977) designed to reduce the surface film was found unnecessary in the culture of *Aplysia brasiliiana* veligers. This moderate veliger loss appears more than acceptable in exchange for removal of complicated sealed systems (KRIEGSTEIN *et al.*, 1974) or mechanical stirring devices, or both, designed to eliminate these losses.

Once individual veligers exhibit visual signs indicative of attainment of metamorphic age they are transferred to a covered glass petri dish (Pyrex No. 3160, 60 × 15 mm) of filtered sea water containing *Isochrysis*. A small tuft of the red alga *Callithamnion* from South Texas is added and veligers are observed for indications of metamorphosis. [Although this alga conforms to the description of *Callithamnion byssoides* Arnott *in* Hooker given by EDWARDS (1970), Dr. Clinton J. Dawes of the University of South

Florida has identified the material (personal communication) as *Callithamnion halliae* Collins.] Metamorphosis was also induced upon exposure of veligers to at least one species of *Polysiphonia*; successful metamorphosis, however, was quite low and results were not encouraging. Veligers under observation are transferred to a petri dish containing fresh sea water and *Callithamnion* every 2 days until feeding is observed. Once feeding begins, the juvenile specimens are transferred daily to fresh water and algae until specimens are large enough to place in small holding tanks. Natural seaweed is fed for 6 to 8 weeks following metamorphosis. At this time specimens may be induced to feed on the commercially available dried seaweed.

RESULTS AND DISCUSSION

Eggs laid by laboratory held *Aplysia brasiliiana* exhibit wide variation in color. While egg masses are generally dark green to light brown in color, both red and yellow strings have been observed. The egg strand is approximately 1 mm in diameter and usually coiled upon itself during the laying process. There are approximately 150 capsules per cm and, though variable, each capsule contains about 24 eggs. Capsules at the beginning or end of an egg string are often empty or contain a reduced number of eggs. Rotation of individual eggs is observed within 4 days following laying. At 8 to 10 days well developed veligers are observed actively moving about in the capsules. This is shortly followed by disintegration of the egg case resulting in the release of large numbers of free swimming veligers.

Veligers are approximately 140 μ m in diameter at hatching. They are active in their movements and exhibit positive phototaxis. Growth is progressive and by 30 to 40 days specimens attain a diameter of approximately 325 to 375 μ m. At this time individuals exhibit a decrease in swimming activity associated with frequent propodial extension or attachment, or both, to the culture container. This is a visual indicator that the veligers have attained the size and age necessary for initiation of metamorphosis. At this time exposure to a freshly collected tuft of the red seaweed *Callithamnion* will trigger the metamorphic process. Veligers will attach and crawl about on the algae by means of the propodium. Individual veligers may remain permanently attached to the seaweed or may briefly remain attached, withdraw and later return. Successful metamorphosis has been attained in 80% of the specimens retained in culture for 55 days.

The onset of metamorphosis is signaled by propodial attachment followed within 24 hours by loss of the velar cilia and retraction of the velar folds (Figure 1a). This is

accompanied by the appearance of 5 to 10 red pigment spots on the upper right surface of the veliger shell (Figure 1b). The number of these pigment spots will eventually increase to about 25 to 30. Loss of the velar cilia terminates the larval ability to filter-feed and swim. This is followed by approximately 4 days during which time the veliger remains attached to the algae. Individuals at this stage exhibit intermittent periods of limited crawling activity. Dislodgement of the veliger during this quiet phase will reveal in some specimens the presence of a small attachment thread. At approximately 2 to 3 days following settlement muscular movement of the radula sac similar

to that exhibited during feeding is observed. This is followed at about 5 days by actual feeding.

The onset of feeding is followed within 48 hours by loss of the operculum. This is accompanied by a rapid increase in size as well as an increase in red pigmentation of the exposed body surface. Along each side of the head a depigmented tract extends anteriorly from the margin of the adult shell to include the outer distal area of the cephalic tentacle (Figure 1c). In these tracts are located the eyes as well as randomly scattered large white pigment granules. These white granules are also common along the upper margin of the newly forming parapodia. The mid-

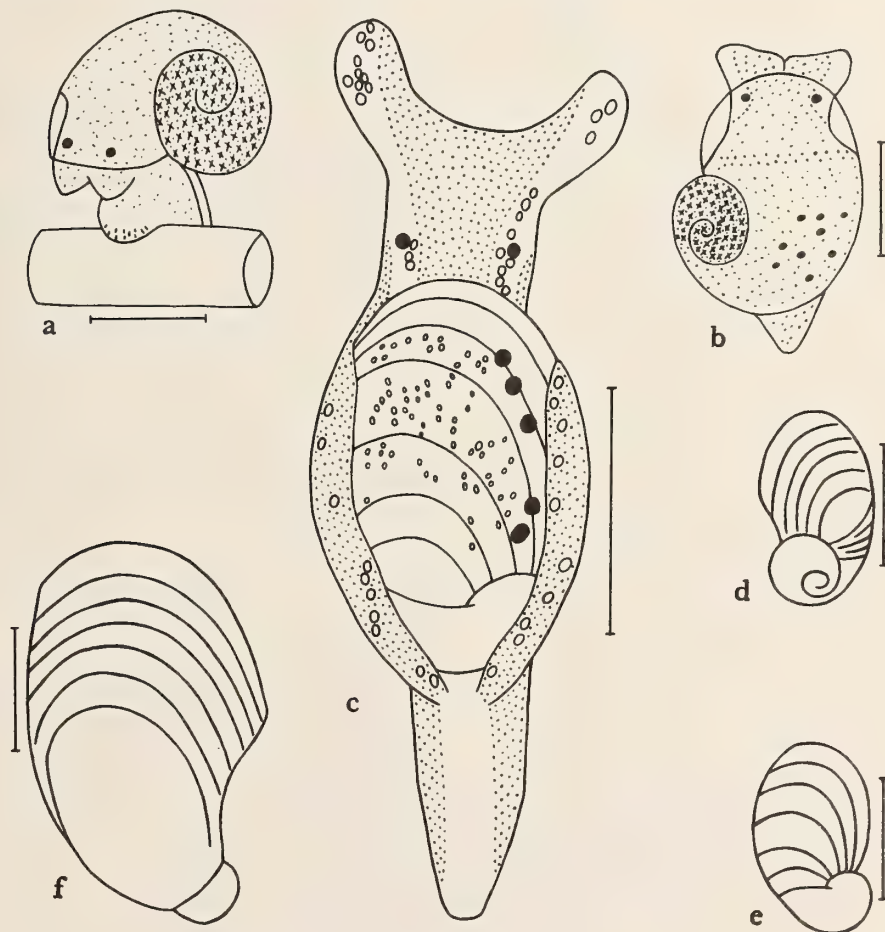


Figure 1

- 1a. Larval stage of *Aplysia brasiliana* 24 hours following the initiation of metamorphosis
 1b. Post-metamorphic stage at 36 hours following the onset of feeding
 1c. Juvenile specimen at 5 days post-feeding
 1d. Ventral view of early developing adult shell with protoconch attached
 1e. Dorsal view of Figure 1d
 1f. Dorsal view of developing shell of 10 day post-feeding juvenile
 Scale of a and b is 0.2mm. Scale of c, d, e, and f is 0.5mm

dorsal surface of the tail (Figure 1c) also lacks red pigmentation. Three to 10 large dark pigment spots begin to form just beneath the surface of the right margin of the newly forming adult shell (Figure 1c). These cells represent the initial formation of the ink gland of the adult.

Although growth rates of individual specimens exhibit a wide degree of variability, most specimens attain 1 mm in total length by 4 days following the onset of feeding. Two small budlike protuberances just posterior to the eyes make their appearance at about 7 to 8 days post-feeding. These structures will enlarge and form the rhinophores of the adult. By about 10 days the dorsal margins of the rapidly enlarging parapodia come in contact and are able to completely enclose the mantle cavity. Specimens are 2.5 to 3 mm in length at this stage and will undulate the parapodia in an effort to assist locomotion along the algae upon which they are feeding.

By 14 days following initiation of feeding, specimens attain lengths of up to 8 mm. The parapodia are greatly enlarged and are folded upon one another to form 2 dorsal siphons. Swimming may be induced by removal of specimens from the algae upon which they are feeding. The distal tips of the now stalk-like rhinophores are cup-shaped. The seminal groove is first noted at this stage. It is poorly developed and only faintly visible. By the 18th day specimens attain a total length of 1.5 cm. At this time the mantle foramen occupies only about one half of the surface area of the adult shell. By 40 days specimens are 3 cm in length and can be induced to feed on the commercial dried seaweed "Laver." Sexual maturity is usually attained by 2 to 3 months post-metamorphosis depending upon food availability and individual growth rate. The above sequence of morphological changes in post-metamorphic development is given for those specimens exhibiting optimal growth rates. Many specimens will be observed to develop less rapidly. Food availability appears to be a major factor in determining individual growth rates.

The development sequence observed in *Aplysia brasiliana* during this study is very similar to that noted for *A. californica* (KRIEGSTEIN *et al.*, 1974) and *A. juliana* and *A. dactylomela* (SWITZER-DUNLAP & HADFIELD, 1977). Major differences are noted in selection of different algal species required as triggering agents for the initiation of metamorphosis.

SUMMARY

Eggs laid by laboratory-held specimens of *Aplysia brasiliana* hatch in about 8 to 10 days. Newly hatched veligers were cultured in filtered sea water at temperatures of 21°

C to 25° C. Cultures were maintained at salinities of 28 to 30 ppt. and fed the unicellular algae *Isochrysis galbana*. Metamorphosis was induced as early as 30 days post-hatching upon exposure to freshly collected specimens of the red seaweed *Callithamnion*. Specimens could be retained in culture for as long as 70 days prior to metamorphosis. Propodial attachment, loss of the velar cilia, and retraction of the velar folds signal the onset of metamorphosis. Feeding begins at 5 days following settlement. This is followed by a rapid increase in growth rate. Sexual maturity is attained at about 2 to 3 months post-metamorphosis, depending upon food availability.

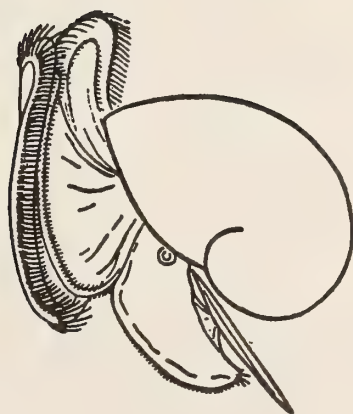
ACKNOWLEDGMENTS

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Selection and Turnover of Coelenterate Nematocysts in Some Aeolid Nudibranchs

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INTRODUCTION

THE STORAGE OF COELENTERATE nematocysts by aeolid nudibranchs is well-known (WRIGHT, 1859; GROSVENOR, 1903; CUÉNOT, 1907; GLASER, 1910; GRAHAM, 1938; KEPNER, 1943; EDMUNDS, 1966; THOMPSON & BENNETT, 1969, 1970; and MARISCAL, 1974); however, the mechanisms involved and the dynamics of the system are poorly understood. GRAHAM (*op. cit.*) and KEPNER (*op. cit.*) described the pathway of nematocysts into the cnidosacs and their uptake by the cnidosac cells. Kepner found that *Aeolis* (= *Cratena*) *pilata* (Gould, 1870) cnidosac cells took up all nematocyst types from the hydroid *Pennaria tiarella* (Ayres, 1854), but maintained only the microbasic mastigophores while digesting the other types. EDMUNDS (*op. cit.*) found that different aeolid species varied in their selectivity of nematocyst types from species that maintained only one type to species that held the entire cnidom of their cnidarian prey. GROSVENOR (*op. cit.*) reported that the nematocyst complement of *Rizzolia* (= *Cratena*) *peregrina* (Deshayes, 1838) was almost entirely replaced a month after shifting the nudibranch to a new hydroid species.

One of us (RMD) spent the spring of 1975 at the Duke Marine Laboratory at Beaufort, North Carolina. During this period *Cratena pilata* were feeding on *Tubularia* spp. instead of *Pennaria* as reported by Kepner (1943). The *Cratena* feeding on *Tubularia* had primarily stenoteles in their cnidosacs versus the microbasic mastigophores present when the prey is *Pennaria*. This observation, as well as the report of different nematocyst preferences with different hydroid prey made by GROSVENOR (1903), suggested that nematocyst selection in aeolid nudibranchs is a complex and dynamic phenomenon which requires further study. The purpose of this report is to describe and

discuss the results of studies on nematocyst selection and turnover in the aeolid nudibranch *Coryphella verrucosa* (Sars, 1829).

MATERIALS AND METHODS

The studies reported here were conducted in the Zoology Department of the University of New Hampshire, Durham, New Hampshire during the summer of 1975. Nudibranchs and their cnidarian prey were collected from floats and pier pilings in Portsmouth Harbor, New Hampshire and benthic communities in Gosport Harbor, Isles of Shoals (43°59'N; 70°37'W) off the New Hampshire coast. Animals were maintained in a recirculating seawater system at 13°C or in an incubator at 5°C. Survival was greater at 5°C, so all experiments were run at this temperature.

Three types of observations were made during the study. First, a series of aeolid species was collected along with their coelenterate prey. The nematocyst complement of each individual was determined by removing a single ceras with fine pointed forceps, squashing it between a glass slide and coverslip and identifying nematocysts extruded from the ceras tip using the key in MARISCAL (1974). The nematocyst complement of each nudibranch was compared to that of the prey species on which it was found in the field.

A cnidosac regeneration experiment was conducted using *Coryphella verrucosa*. This species was used because it is common and eats a variety of coelenterate prey. The experiment consisted of removing the tips of all the cerata anterior to the heart and then allowing the test subjects to feed on the hydroid *Hydractinia echinata* Fleming, 1828. Squashes were made of 3 cerata anterior to and posterior (controls) to the heart on each of the 5 exper-

imental animals. The presence of a large number of nematocysts in ceras tip squash mounts was used as an indicator of cnidosac regeneration.

The third experiment consisted of isolating groups of 5 nudibranchs, each with previously determined nematocyst complements, with different hydroid species and monitoring by ceras-squash preparations any changes in the nematocyst complement in each group. The first 25 identifiable nematocysts were recorded in each squash preparation.

RESULTS AND OBSERVATIONS

The nematocyst complements of several aeolid nudibranch species collected on known coelenterate prey are summarized in Table 1. As is obvious from this table, many aeolid species are quite specific in their selection of nematocyst types and the type varies according to the prey species being consumed. *Cratena pilata* selects microbasic mastigophores when eating *Pennaria* (KEPNER, 1943) and steno-

Table 1

Summary of nematocyst types observed in the cnidosacs of several aeolid nudibranchs as compared with their coelenterate prey. Where more than one type was present, the dominant form is indicated by an asterisk (*).

Nudibranch species	Coelenterate Prey	Nematocysts identified in Coelenterate	Nematocysts identified in Cnidosacs
<i>Cratena pilata</i>	<i>Tubularia</i> spp.	stenoteles basitrichous isorhizas holotrichous or atrichous isorhizas desmonemes	stenoteles* basitrichous isorhizas
<i>Aeolidia papillosa</i>	<i>Metridium senile</i>	spirocysts basitrichous isorhizas microbasic mastigophores microbasic amastigophores atrichous isorhizas holotrichous isorhizas	microbasic amastigophores basitrichous isorhizas
<i>Catriona aurantia</i>	<i>Tubularia</i> spp.	stenoteles basitrichous isorhizas holotrichous or atrichous isorhizas desmonemes	stenoteles basitrichous isorhizas
<i>Cuthona nana</i>	<i>Hydractinea echinata</i>	desmonemes microbasic euryteles microbasic mastigophores holotrichous or atrichous isorhizas	microbasic mastigophores
<i>Facelina bostoniensis</i>	<i>Tubularia</i> spp.	stenoteles basitrichous isorhizas holotrichous or atrichous isorhizas desmonemes	stenoteles
<i>F. bostoniensis</i>	<i>Eudendrium</i> spp.	microbasic euryteles microbasic mastigophores	microbasic mastigophores microbasic euryteles*
<i>Coryphella verrucosa</i>	<i>Hydractinea echinata</i>	desmonemes microbasic euryteles microbasic mastigophores isorhizas (holotrichous or atrichous)	microbasic mastigophores* desmonemes
<i>C. verrucosa</i>	<i>Obelia geniculata</i>	basitrichous isorhizas	basitrichous isorhizas
<i>C. verrucosa</i>	<i>Tubularia crocea</i>	stenoteles basitrichous isorhizas holotrichous or atrichous isorhizas	stenoteles* basitrichous isorhizas
<i>C. verrucosa</i>	<i>Lucernaria</i> spp.	Microbasic euryteles atrichous isorhizas	microbasic euryteles

teles when feeding on *Tubularia*. *Coryphella verrucosa* also stores stenoteles from *Tubularia*, but selects microbasic mastigophores when feeding on *Hydractinia*, basitrichous isorhizas from *Obelia* spp. and microbasic euryteles when eating the stauromedusan *Lucernaria* sp.

There appears to be a consistent pattern of preference for certain nematocyst types in several nudibranch species when consuming the same prey species. *Cuthona nana* (Alder & Hancock, 1842) and *Coryphella verrucosa* both store microbasic mastigophores when eating *Hydractinia*, while *Coryphella verrucosa*, *Cratena pilata* and *Catriona aurantia* (Alder & Hancock, 1842) select stenoteles when feeding on *Tubularia* spp.

The regeneration experiment provided two significant results. Nematocysts were observed in regenerating cerata in all animals within 12 days, indicating the presence of functional cnidosacs. By this time the cnidosacs of the posterior, or control cerata, contained only microbasic mastigophores instead of the euryteles present at the start of the experiment. There had been a total replacement of nematocysts in less than 12 days.

An experiment was then performed in which a group of *Coryphella verrucosa*, collected from an area containing *Lucernaria* sp., *Obelia* sp. and *Tubularia crocea*, were

isolated and fed specific hydroid species; the nematocyst complements of the nudibranchs' cnidosacs were then monitored. Table 2 summarizes the results of this experiment. In each case, the turnover time was 3 to 4 days. The ceras squashes often contained more than one nematocyst type, even after the nematocyst complement had become dominated by a new type. In the case of the *Obelia*, which has only basitrichous isorhizas, closer examination turned up some actinulae larvae of *Tubularia* among the colonies. There were no contaminating hydroids in the other setups, but the nudibranchs were not isolated from food for any period of time before the ceras squashes were made; it is likely, therefore, that other nematocysts seen were from a recent meal and had not been processed as yet.

DISCUSSION

One of the more fascinating aspects of the association between aeolid nudibranchs and coelenterates is the storage and utilization of functional nematocysts. The position of the cnidosacs at the tips of the cerata and the fact that nematocysts are ejected when the nudibranch is

Table 2

Results of experiment to determine selectivity and turnover rates of nematocysts in *Coryphella verrucosa* fed three hydroid species. The nudibranchs were found associated with the stauromedusan *Lucernaria* sp. though *Obelia* spp. and *Tubularia crocea* were also present.

Prey species	Nematocysts Observed in Cnidosacs				Minimum Time
	Start of Experiment		After eight to ten days		
	Dominant Form	Also seen	Dominant Form	Also seen	Turnover
<i>Hydractinea echinata</i>	microbasic euryteles		microbasic mastigophores	stenoteles ¹ desmonemes	4
<i>Tubularia crocea</i>	microbasic euryteles	stenoteles microbasic mastigophores basitrichous isorhizas atrichous isorhizas	stenoteles	euryteles ¹ microbasic mastigophores basitrichous isorhizas	4
<i>Obelia geniculata</i>	microbasic euryteles	stenoteles microbasic mastigophores atrichous isorhizas	basitrichous isorhizas	stenoteles	3

¹—seen in only one specimen.

disturbed has led to the general conclusion that they must be used for defense by aeolids (GARSTANG, 1894; KEPNER, 1943; EDMUNDS, 1966; HARRIS, 1973). In fact, there is to date only one documentation of a defensive function for nematocysts in aeolids based on experimental evidence. ALLEN (1976) reported finding basitrichous isorhizas in the puffed and necrotic mouth tissue of a shiner surfperch *Cymatogaster aggregata* Gibbons, 1854, that had bitten and rejected a *Hermisenda crassicornis* (Eschscholtz, 1831).

Several authors (KEPNER, 1943; EDMUNDS, 1966; THOMPSON & BENNETT, 1969) have suggested that the selection of specific nematocyst types is an adaptation to store the most effective nematocysts against predators. EDMUNDS (*op. cit.*) suggested that different nematocyst types were selected for in response to different predators — penetrants against fish predators and desmonemes for crustaceans.

THOMPSON & BENNETT (1969, 1970) proposed that aeolids maintain a supply of certain nematocyst types independent of the number of different coelenterates preyed upon, stating that *Glaucus atlanticus* (Forster, 1777) and *Glaucilla marginata* (Bergh, 1868) employ *Physalia* nematocysts for defense, usually digesting those from *Porpita* and *Velella*. GROSVENOR (1903) gave the first indication that different nematocysts might be incorporated from different prey by stating that the nematocyst complement could vary among individuals of the same species. The results of this study confirm Grosvenor's observations and provide evidence that at least some aeolid species incorporate specific nematocyst types with each prey species and the nematocyst type varies from prey species to prey species. KEPNER (1943) reported that *Cratena pilata* stored microbasic mastigophores when feeding on *Pennaria tiarella* and we found that *C. pilata* selects stenoteles when it eats *Tubularia* spp. MARISCAL (1974) stated that *Aeolidia papillosa* (Linnaeus, 1761) stored basitrichous isorhizas when feeding on *Epiactis prolifera* Verrill, 1869, while we found microbasic mastigophores and basitrichous isorhizas in specimens associated with *Metridium senile* (Linnaeus, 1767) *Coryphella verrucosa* selects 4 separate nematocyst types from 4 prey species. In regard to Thompson & Bennett's observations, the aeolids may not have been selecting against the nematocysts from *Porpita* and *Velella*, but had simply fed on *Physalia* most recently and the nematocysts from the other coelenterates were in the process of being replaced.

Several aspects of the selection mechanism appear to be of particular interest, specifically the rate of turnover and the significance of selecting a distinct nematocyst type. GROSVENOR (1903) reported that the replacement in ne-

matocyst complement after changing the prey species in *Cratena peregrina* was about 30 days. The results of this study suggest the process of replacement may occur much faster. When considering KEPNER's (1943) observations that nematocysts were present in the cnidosacs of *Cratena pilata* 25 minutes after feeding and that none remained in the stomach after 35 minutes, the faster turnover rate does not seem unreasonable.

The fact that a process of replacing unused nematocysts is occurring and that the turnover rate is relatively quick suggests that there may be a limit on the length of time a nematocyst remains functional in the nudibranchs' cnidocyte analogue, the cnidosac cells. It is possible that nematocysts which are very complex cell organelles may lose their ability to fire over time. If this is the case, then selection pressure should favor a rapid turnover of nematocysts. Starved nudibranchs still contain nematocysts after several weeks, which suggests that the turnover rate varies according to the nutritional state of the nudibranch. If nematocysts are stored primarily for defensive purposes, then natural selection should favor maintaining a nematocyst complement even though its effectiveness may be decreasing over time. Therefore, while the number of functional nematocysts might decrease, a percentage will still be able to discharge, providing the aeolid with more protection than if all nematocysts had been discarded leaving none for defense. It must be kept in mind that nematocyst utilization is only one of several defensive mechanisms typically employed by aeolid nudibranchs, including cryptic coloration, autotomy of cerata, and secretions from ceratal glands (EDMUNDS, 1966).

Little information is available on the turnover of nematocysts in coelenterates. BODE & FLICK (1976) found that nematocysts in *Hydra attenuata* (Pallas) are replaced in 7 to 9 days, so it may be that even in cnidocysts, nematocysts become nonfunctional in a relatively short period of time. The information available suggests that studies of nematocyst dynamics in coelenterates may provide some interesting insights into nematocyst biology.

There appear to be two possible mechanisms for the turnover of nematocysts in nudibranch cnidosacs. The first explanation is an extension of the mechanism for nematocyst selection (KEPNER, 1943). Cnidosac cells would simply continue to engulf new nematocysts as long as they were available, digesting non-preferred types and holding preferred ones. A second possibility is that new cnidosac cells are continuously being produced at the neck of the cnidosac and older cells are sloughed off or somehow eliminated. Since starved nudibranchs maintain nematocysts much longer than fed animals, cell production may decrease when coelenterate prey, and therefore nematocysts,

were not available. The most likely explanation for the mechanism of nematocyst turnover seems to be a combination of both cell proliferation and turnover within individual cells.

An obvious question raised by this study is why a different type of nematocyst is selected from each prey genus or species if presumably the same types of nematocysts are available? Nematocysts are cell organelles with several functions in coelenterates including offense, defense and adhesion (MARISCAL, 1974), but little information is available on the function of specific nematocyst types and how this might vary from species to species. The selection of distinct nematocyst types for each prey species by a nudibranch suggests a complex recognition mechanism in cnidosac cells. The fact that the same cell selectively maintains stenoteles from one prey species, microbasic mastigophores from another, basitrichous isorhizas from a third and microbasic euryteles from a fourth prey species also indicates the nematocysts from different species may not be as similar in function as their morphology might suggest. Stenoteles are superficially similar in most hydroid species, but their function and the stimuli which induce firing may vary significantly. *Cratena pilata* stores stenoteles when it feeds on *Tubularia*, but not when it eats *Pennaria* (KEPNER, 1943). An alternative hypothesis might be that cnidosac cells are selecting for relative abundance of nematocyst types in any given prey species. However, this hypothesis does not account for the fact that only one type is maintained in each case and it neglects the functional explanation for why nematocysts are stored-defense (KEPNER, 1943; EDMUNDS, 1966; ALLEN, 1976).

Aeolids from separate families feeding on the same prey species select the same nematocyst type; this suggests that nudibranchs occurring in the same habitat and overlapping in their prey preferences may also be subject to similar selection pressure from predators, resulting in their picking the same type. KEPNER (1943) proposed that the microbasic mastigophores of *Pennaria tiarella* were more effective predator deterrents for *Cratena pilata* than the larger penetrants which appeared to be stenoteles. If Kepner is correct, then the stenoteles of *Tubularia* spp. and microbasic mastigophores in *Hydractinia* should be the most effective predator deterrents in these hydroids.

Not all aeolids show the same specificity as has been shown for most of the species discussed in this report. EDMUNDS (1966) found that some aeolid species did not select specific nematocyst types, but tended to have several types in the cnidosacs at any one time. MARISCAL (1974) found 2 types of nematocysts in the cnidosacs of *Hermisenda crassicornis* and one type in *Aeolidia papillosa*, and *Facelina bostoniensis* (Couthouy, 1838) may store

more than one nematocyst type when feeding on certain prey species.

Coryphella verrucosa is a generalist in that it eats a variety of hydroid species and stauromedusans, but individuals do concentrate their efforts on locally and temporally abundant species as predicted in ecological theory (EMLEN, 1966, 1968; MACARTHUR & PIANKA, 1966). While cnidosac cells in many aeolids store only one type of nematocyst from each prey species, they ingest all types and digest those types not maintained; this suggests that it is energetically advantageous to engulf and digest the nonpreferred nematocyst types rather than to engulf only the type to be utilized for defense. Another implication of this process is that the site of recognition and selection is within the cytoplasm rather than on the cell membrane where most chemoreception takes place.

In conclusion, the results of this study show that nematocyst utilization in aeolid nudibranchs is a dynamic and complex phenomenon which involves selection of specific types determined by the prey species consumed and that there is a rapid turnover of stored nematocysts. A number of aspects of this system would seem to offer promising avenues for further research.

SUMMARY

Observations on the nematocyst complement of several aeolid nudibranchs resulted in the findings that at least a number of aeolid species select specific nematocyst types from their coelenterate prey and that different nematocyst types are stored when different prey species are eaten.

A regeneration experiment showed that cnidosac replacement in *Coryphella verrucosa* was complete in less than 12 days at 5°C. The turnover of nematocyst types was also found to be much faster than previously reported.

Groups of *Coryphella verrucosa* were fed different hydroid prey and the turnover of nematocysts was followed. *Coryphella verrucosa* selected a distinct nematocyst type from each of the 4 prey species used and the turnover of nematocysts was complete in 3 to 5 days.

It is postulated that nematocysts stored in cnidosac cells are turned over quickly because nematocysts have a finite viability as is suggested by BODE & FLICK's (1976) studies on *Hydra*.

The selection of the nematocyst type by several species of nudibranchs eating the same coelenterate species and preference for different nematocyst types in different prey suggests that nudibranch-hydroid associations may be a useful model for studying the role of nematocysts both in coelenterates and in their nudibranch predators.

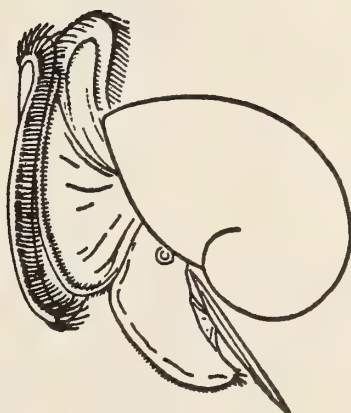
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Additional Notes on the Food of Some California Nudibranchs with a Summary of Known Food Habits of California Species

BY

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A FEW PUBLICATIONS have dealt extensively with nudibranch food habits (*e. g.*, MILLER, 1961, 1962; SWENNEN, 1961; THOMPSON, 1964), but these have treated few of the species which occur in California. This paper attempts to summarize what has previously been reported concerning food habits of species that occur in California (see Table 1) and presents additional data for some species.

The new data on food items of nudibranchs were obtained in the field while collecting nudibranchs for taxonomic and ecological studies and are not, therefore, the results of a deliberate extensive food habit study. However, we believe they should still prove useful in further investigations of nudibranch food habits. We report herein not only actual observations of ingestion of prey, but also situations in which the evidence suggests strongly that the nudibranch species has consumed a given prey species.

ADDITIONAL FOOD NOTES

On 19 December 1976 at Pescadero Point, San Mateo County, California, a single specimen of *Antipella barbarensis* was found on a colony of the bryozoan *Bugula californica* Robertson, 1905. The nudibranch was maintained for 9 days in a culture dish with the bryozoan. During this period, the nudibranch increased from the original 3 mm in total length to 12 mm. The animal was observed to eat the lophophores of the bryozoan.

Over a period of 3 years, several specimens of *Laila cockerelli* were found on the encrusting bryozoan *Hincksiina velata* (Hincks, 1881). When found on the bryozoan, the zoecia immediately beneath the anterior end of the nudibranch were empty, while the remainder of the colony was still intact, suggesting this species consumes the bryozoan.

In the central California area, we have observed *Tritonia festiva* to be most common where the alcyonarian *Clavularia*

sp. is also most common. Since tritoniids are known to feed on alcyonarians (WICKSTEN & DEMARTINI, 1973; GOMEZ, 1973; THOMPSON, 1971), specimens of *T. festiva* and *Clavularia* *sp.* were placed together in a culture dish of sea water. Of the 4 specimens of *T. festiva* that were offered *Clavularia* *sp.*, 3 were each seen to eat one or more polyps. We have not observed them eating any other organism.

On 2 November 1975 at Carmel Point, Monterey County, California, 2 specimens of *Ancula pacifica* were found, together with their nidosomes on the entoproct *Barentsia ramosa* (Robertson, 1900). Subsequent observation in the laboratory indicated they would eat the calyx of the entoproct.

On 27 January 1976, 2 specimens of *Aldisa sanguinea* were found on the sponge *Hymendesmia brepha* (deLaubenfels, 1930). Immediately beneath the mouth of both specimens was a depression which had been rasped into the sponge.

A single specimen of *Anisodoris nobilis* was found on the sponge *Lissodendoryx firma* (Lambe, 1895) with a depression immediately beneath the mouth of the nudibranch. *Anisodoris nobilis* has also been reported to feed on numerous other species of sponges (see Table 1).

Over a span of 3 years, numerous specimens of *Cadlina modesta* have been found on the sponge *Aplysilla glacialis* (Dybowski, 1880), often accompanied by their nidosomes. Most specimens have been found with a depression rasped into the sponge immediately beneath them, and 2 specimens were seen eating the sponge. Two specimens of *C. flavomaculata* were also found on *A. glacialis* with depressions rasped into the sponge beneath them.

A single specimen of *Discodoris heathi* was found on the sponge *Adocia gellindra* (deLaubenfels, 1932) (as *Reniera* *sp.* in SMITH & CARLTON, 1975). There was a large depression rasped into the sponge beneath the nudibranch.

On 26 October 1975 at Morro Bay, San Luis Obispo County, California, 3 specimens of *Hallaxa chani* were

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Table 1

Summary of nudibranch-food associations for species occurring in California.

^(P) indicates personal observation by the authors.

Nudibranch Species	Food Item
DORIDACEA	
Anadoridacea	
SUCTORIA	
CORAMBIDAE	
<i>Corambe pacifica</i>	<i>Membranipora villosa</i> ^(32, 33) on <i>Membranipora serrilamella</i> ⁽³⁸⁾
<i>Doridella steinbergae</i>	<i>Membranipora</i> sp. ⁽³⁶⁾ <i>Membranipora serrilamella</i> ⁽³⁰⁾ <i>Membranipora membranacea</i> ⁽³²⁾ <i>Membranipora</i> spp. ⁽³⁰⁾
OKENIDAE	
Anculinae	
<i>Ancula pacifica</i>	<i>Barentsia ramosa</i> ^(P)
Hopkinsiinae	
<i>Hopkinsia rosacea</i>	<i>Eurystomella bilabiata</i> ^(57, P)
ONCHIDORIDIDAE	
<i>Acanthodoris brunnea</i>	bryozoans ⁽⁷⁵⁾
<i>Acanthodoris nanaimoensis</i>	compound ascidians ^(P)
<i>Acanthodoris pilosa</i>	<i>Flustrellidra hispida</i> ^(46, 63) <i>Alcyonidium hirsutum</i> , <i>Callopora dumerili</i> ⁽⁴⁰⁾ <i>Alcyonidium gelatinosum</i> ^(21, 40) <i>Alcyonidium polyomm</i> ^(40, 62) <i>Cryptosula pallasiana</i> ⁽¹¹⁾ on <i>Alcyonidium gelatinosum</i> ^(62, 63) on <i>Alcyonidium polyomm</i> ^(40, 61)
<i>Onchidoris bilamellata</i>	<i>Balanus balanoides</i> ^(2, 40, 48, 61) <i>Balanus crenatus</i> ^(2, 61) <i>Balanus porcatus</i> ⁽⁴⁰⁾ <i>Elminius modestus</i> ⁽⁶¹⁾ barnacles ^(11, P)
<i>Onchidoris muricata</i>	<i>Alcyonidium polyomm</i> ⁽⁶¹⁾ <i>Celleporella hyalina</i> , <i>Cryptosula pallasiana</i> , <i>Electra pilosa</i> , <i>Escharella immersa</i> , <i>Microporella ciliata</i> , <i>Porella concinna</i> , <i>Schizomavella linearis</i> , <i>Schizoporella unicornis</i> , <i>Smittina reticulata</i> , <i>Umbonula littoralis</i> ⁽⁴⁰⁾ <i>Membranipora membranacea</i> ^(2, 40, 62, 63) on <i>Reginella mucronata</i> ^(P)
NONSUCTORIA	
TRIOPHIDAE	
Triophinae	
<i>Triopha carpenleri</i>	<i>Caulibugula ciliata</i> , <i>Membranipora membranacea</i> , <i>Cauloramphus spiniferum</i> , <i>Scrupocellaria californica</i> , <i>Bugula mollis</i> , <i>Crisia occidentalis</i> , <i>Tricellaria</i> sp. ⁽⁴⁵⁾ ectoprocts ⁽²³⁾

Table 1 (continued)

Nudibranch Species	Food Item
<i>Triopha maculata</i>	<i>Scrupocellaria californica</i> , <i>Dendrobeania laxa</i> , <i>Caulibugula ciliata</i> , <i>Bugula mollis</i> , <i>Tricellaria</i> sp., <i>Crisia occidentalis</i> , <i>Filicrisia fran-</i> <i>ciscana</i> ⁽⁴⁵⁾
POLYCERIDAE	
<i>Laila cockerelli</i>	<i>Hincksina velata</i> ^(P)
<i>Polycera atra</i>	<i>Bugula</i> ⁽³⁸⁾ <i>Membranipora membranacea</i> ⁽⁷⁴⁾ <i>Membranipora</i> , <i>Lophogorgia chilensis</i> ⁽⁵¹⁾ on <i>Bugula pacifica</i> ^(P)
<i>Polycera hedgpethi</i>	on <i>Bugula pacifica</i> ^(P)
<i>Polycera zosteræ</i>	<i>Membranipora</i> sp., ⁽⁵⁴⁾ on <i>Bowerbankia gracilis</i> var. <i>aggregata</i> ⁽⁸⁰⁾
Eudoridacea	
CADLINIDAE	
Cadlininae	
<i>Cadlina flavomaculata</i>	<i>Aplysilla glacialis</i> ^(P)
<i>Cadlina luteomarginata</i>	<i>Halichondria panicea</i> , <i>Myxilla incrustans</i> , <i>Higginsia</i> sp. ⁽⁷⁾
<i>Cadlina modesta</i>	<i>Aplysilla glacialis</i> ^(P)
CHROMODORIDIDAE	
<i>Chromodoris mcfarlandi</i>	on <i>Gellius</i> sp., on <i>Haliclona</i> sp. ⁽⁷⁾
<i>Chromodoris porterae</i>	on <i>Dysidea ambliæ</i> ^(P)
<i>Hypselodoris californiensis</i>	<i>Stelletta estrella</i> , <i>Haliclona</i> sp. ⁽³⁷⁾ on <i>Dysidea ambliæ</i> ^(P)
ACTINOCYCLIDAE	
<i>Hallaxa chani</i>	<i>Didemnum carnulentum</i> ^(P)
ALDISIDAE	
<i>Aldisa sanguinea</i>	on <i>Ophlitaspongia pennata</i> ⁽¹⁸⁾ <i>Hymendesmia brepha</i> ^(P)
ROSTANGIDAE	
<i>Rostanga pulchra</i>	<i>Esperiopsis originalis</i> ⁽¹⁵⁾ <i>Plocamia lithophoenix</i> , <i>P. karykina</i> , <i>Acarnus erithacus</i> ^(58, 71) <i>Ophlitaspongia pennata</i> ^(15, 58, 71) on <i>Isociona lithophoenix</i> , on <i>Esperiopsis originalis</i> ⁽⁷⁾
ARCHIDORIDIDAE	
<i>Archidoris montereyensis</i>	<i>Halichondria panicea</i> ^(7, 19, P)
<i>Archidoris odhneri</i>	<i>Halichondria panicea</i> ^(7, 54) <i>Myxilla incrustans</i> , <i>Mycale adhaerens</i> ⁽⁷⁾ <i>Stylissa stipitata</i> , <i>Tedania</i> sp., <i>Craniella</i> sp., <i>Syringella amphispicula</i> ⁽⁵⁴⁾
DISCODORIDIDAE	
<i>Discodoris heathi</i>	on <i>Halichondria panicea</i> , on <i>Myxilla incrustans</i> ⁽⁷⁾ <i>Adocia gellindra</i> ^(P)
<i>Anisodoris nobilis</i>	<i>Myxilla agennes</i> , <i>Paresperella psila</i> , <i>Zygherpe hyaloderma</i> , <i>Mycale</i> <i>macginitiei</i> , <i>Prianos</i> sp. ⁽⁵⁷⁾ <i>Mycale adhaerens</i> , <i>Haliclona permollis</i> , <i>Halichondria panicea</i> ⁽⁷⁾ <i>Lissodendoryx firma</i> ^(P)

Table 1 (continued)

Nudibranch Species	Food Item
<i>Diaulula sandiegensis</i>	on <i>Halichondria panicea</i> , on <i>Myxilla incrustans</i> , <i>Petrosia dura</i> ⁽⁷⁾ <i>Halichondria bowerbanki</i> ^(P) <i>Haliclona permollis</i> ^(7, 17) <i>Haliclona</i> sp. ⁽¹⁹⁾
Porodoridae	
DENDRODORIDIDAE	
<i>Doriopsilla albopunctata</i>	<i>Cliona celata</i> , <i>Ficulina suberea</i> , <i>Acarnus erithacus</i> , <i>Suberites</i> sp. ⁽⁸⁷⁾
DENDRONOTACEA	
TRITONIDAE	
<i>Tritonia diomedea</i>	<i>Virgularia</i> sp. ⁽⁶⁴⁾ <i>Ptilosarcus gurneyi</i> ⁽⁷⁰⁾
<i>Tritonia festiva</i>	<i>Clavularia</i> sp. ^(P) <i>Ptilosarcus gurneyi</i> ^(19, 70) <i>Lophogorgia chilensis</i> ⁽¹⁹⁾
<i>Tochuina tetraquetra</i>	<i>Gersemia rubiformis</i> ⁽⁶⁸⁾ <i>Ptilosarcus gurneyi</i> ^(64, 70)
DENDRONOTIDAE	
<i>Dendronotus albus</i>	on <i>Plumularia</i> sp. ^(P)
<i>Dendronotus diversicolor</i>	on <i>Abietinaria</i> spp., on <i>Sertularella tricuspidata</i> , on <i>Hydrallmania distantis</i> ⁽⁵¹⁾
<i>Dendronotus frondosus</i>	<i>Tubularia indivisa</i> ^(40, 61) <i>Tubularia larynx</i> ^(9, 40) <i>Dynamena pumila</i> , <i>Hydrallmania falcata</i> ^(84, 60) <i>Sertularia argentea</i> ⁽⁴⁰⁾ <i>Sertularia cupressina</i> ⁽⁶¹⁾ on <i>Abietinaria abietina</i> ⁽⁸⁴⁾ on <i>Sertularia argentea</i> ^(14, 47) <i>Coryne</i> sp. ⁽⁷⁵⁾ on <i>Aglaophenia</i> ⁽⁷⁵⁾ on <i>Sertularia cupressina</i> ⁽¹⁴⁾ <i>Hydractinia echinata</i> ⁽⁸⁹⁾ <i>Tubularia crocea</i> , <i>Obelia</i> spp. ⁽¹¹⁾ <i>Sertularia dichotoma</i> ⁽⁸²⁾ <i>Botryllus schlosseri</i> ⁽⁴⁹⁾
<i>Dendronotus iris</i>	<i>Pachycerianthus fimbriatus</i> ^(60, P)
<i>Dendronotus subramosus</i>	<i>Aglaophenia struthionides</i> ⁽⁵¹⁾
TETHYIDAE	
<i>Melibe leonina</i>	Gammarids, Caprellids ⁽⁸⁵⁾ Copepods ^(1, 85, 74) Amphipods ⁽⁷⁴⁾
DOTONIDAE	
<i>Doto amyra</i>	on <i>Obelia</i> ⁽⁷⁵⁾

Table 1 (continued)

Nudibranch Species	Food Item
ARMINACEA	
EUARMINOIDEA	
ARMINIDAE	
<i>Armina californica</i>	<i>Renilla koellikeri</i> ^(5, 46, 63) <i>Renilla 'amethystina'</i> ⁽³⁸⁾ <i>Ptilosarcus gurneyi</i> ^(70, P)
PACHYGNATHA	
DIRONIDAE	
<i>Dirona albolineata</i>	<i>Margarites pupillus</i> , <i>M. helycinus</i> , <i>Lacuna carinatus</i> , ectoprocts, hydroids, small crustaceans, sponges, barnacles, tunicates ⁽⁵²⁾
<i>Dirona picta</i>	on <i>Thaumatoportella</i> sp. ^(P) <i>Aglaophenia</i> sp. ⁽⁷⁶⁾ <i>Celleporella hyalina</i> ⁽⁷⁵⁾
ZEPHYRINIDAE	
<i>Antiopella barbarensis</i>	<i>Bugula californica</i> ^(P) <i>Corymorpha palma</i> ⁽⁷⁴⁾
AEOLIDACEA	
EUEOLIDOIDEA	
PLEUROPROCTA	
CORYPHELLIDAE	
<i>Coryphella trilineata</i>	on <i>Eudendrium</i> sp., on <i>Tubularia crocea</i> ^(P)
FLABELLINIDAE	
<i>Flabellinopsis iodinea</i>	<i>Eudendrium ramosum</i> ⁽⁵⁷⁾ <i>Diplosoma pizoni</i> ⁽⁷⁴⁾
ACLEIOPROCTA	
EUBRANCHIDAE	
Cumanotinae	
<i>Cumanotus beaumonti</i>	<i>Tubularia crocea</i> ^(P)
Eubbranchinae	
<i>Eubbranchus olivaceus</i>	on <i>Obelia longissima</i> ⁽⁴⁶⁾
<i>Eubbranchus rustyus</i>	on <i>Hydractinia</i> sp. ⁽⁵²⁾ on <i>Plumularia lagenifera</i> ⁽⁵⁴⁾ on <i>Obelia</i> ⁽⁷⁵⁾
CUTHONIDAE	
Precuthoninae	
<i>Precuthona divae</i>	on <i>Hydractinia</i> sp. ^(10, 30, P)
Cuthoninae	
<i>Tenellia pallida</i>	<i>Cordylophora lacustris</i> ⁽⁴⁴⁾ <i>Gonothyraea loveni</i> ⁽⁵⁰⁾ <i>Protohydra leuckarti</i> , <i>Psammohydra</i> sp. ⁽⁵⁵⁾ on <i>Obelia dichotoma</i> ⁽¹²⁾ <i>Laomedea loveni</i> , <i>L. longissima</i> , <i>Cordylophora caspia</i> ⁽⁶¹⁾ <i>Obelia</i> , <i>Podocoryne</i> ⁽⁵⁸⁾
<i>Catriona alpha</i>	<i>Tubularia marina</i> , <i>T. sp.</i> , on <i>Syncoryne eximia</i> , on <i>Obelia</i> sp. ⁽⁵⁴⁾ on <i>Tubularia crocea</i> ^(P)

Table 1 (continued)

Nudibranch Species	Food Item
FIONIDAE	
<i>Fiona pinnata</i>	<i>Porpita</i> sp. ⁽³⁴⁾ <i>Lepas anatifera</i> ^(P) barnacles ⁽¹⁶⁾ <i>Lepas</i> ^(8, 58) <i>Lepas anserifera</i> ⁽⁶⁾ <i>Velella velella</i> ^(4, 16, 34) <i>Velella spirans</i> ⁽⁸⁷⁾ <i>Velella</i> ^(8, 57)
CLEIOPROCTA	
FACELINIDAE	
<i>Hermisenda crassicornis</i>	<i>Ptilosarcus gurneyi</i> ⁽⁷⁰⁾ <i>Obelia</i> spp., canibalistic ⁽²³⁾
<i>Phidiana pugnax</i>	<i>Hydractinia</i> sp. ^(P)
AEOLIDIIDAE	
<i>Aeolidia papillosa</i>	<i>Tealia crassicornis</i> ^(15, 39, 67) <i>Actinia</i> , "Anthea" ⁽¹⁶⁾ <i>Actinia equina</i> ^(15, 40, 61, 72) <i>Anemonia sulcata</i> ^(15, 40) <i>Diadumene cincta</i> ⁽⁶¹⁾ ' <i>Metridium marginatum</i> ' ⁽⁵⁶⁾ <i>Metridium senile</i> ^(15, 61, 63, 67, 72, P) <i>Sagartia troglodytes</i> ^(40, 61) <i>Sagartiogeton undata</i> ⁽⁶¹⁾ <i>Stomphia coccinea</i> ⁽³⁵⁾ <i>Tealia felina</i> ^(15, 40, 61, 63) <i>Tubularia indivisa</i> ⁽⁴⁰⁾ <i>Tealiopsis stella</i> ⁽²³⁾ <i>Metridium dianthus</i> ⁽¹¹⁾ <i>Epiactis prolifera</i> , <i>Anthopleura xanthogrammica</i> , <i>Diadumene luciae</i> , <i>Tealia coriacea</i> , <i>Anthopleura artemisia</i> , <i>Corynactis californica</i> ⁽⁶⁷⁾ <i>Actinothoe sphyrodeta</i> , <i>Anthopleura balli</i> , <i>Sagartia elegans</i> , <i>Cereus</i> <i>pedunculatus</i> , <i>Aiptasia couchi</i> , <i>Corynactis viridis</i> ⁽¹⁵⁾ <i>Anthopleura elegantissima</i> ^(15, 32, 67)
<i>Aeolidiella takanosimensis</i>	<i>Sagartia</i> ⁽⁵⁸⁾
<i>Cerberilla mosslandica</i>	burrowing anemone ⁽⁵⁸⁾
SPURILLIDAE	
<i>Spurilla oliviae</i>	<i>Metridium senile</i> ^(28, P)
<i>Spurilla chromosoma</i>	<i>Metridium senile</i> ⁽²³⁾

In order to conserve space the full citation of the taxa discussed and listed was excluded from the table. It is given in alphabetical order below.

Mollusca

Acanthodoris nanaimoensis O'Donoghue, 1921; *A. pilosa* (Abildgaard, 1789); *Aeolidia papillosa* (Linnaeus, 1761); *Aeolidiella*

takanosimensis Baba, 1930; *Aldisa sanguinea* (Cooper, 1862); *Anacula pacifica* MacFarland, 1905; *Anisodoris nobilis* (MacFarland, 1905); *Antiopeella barbarensis* (Cooper, 1863); *Archidoris montereyensis* (Cooper, 1862); *A. odhneri* (MacFarland, 1966); *Armina californica* (Cooper, 1862)
Cadlina flavomaculata MacFarland, 1905; *C. luteomarginata* MacFarland, 1966; *C. modesta* MacFarland, 1966; *Catriona alpa* (Baba

* Hamatani, 1963); *Cerberilla mosslandica* McDonald & Nybakken, 1975; *Chromodoris mcfarlandi* Cockerell, 1902; *C. porterae* Cockerell, 1902; *Corambe pacifica* MacFarland & O'Donoghue, 1929; *Coryphella trilineata* O'Donoghue, 1921; *Cumanotus beaumonti* (Eliot, 1906)
Dendronotus albus MacFarland, 1966; *D. diversicolor* Robilliard, 1970; *D. frondosus* (Ascanius, 1774); *D. iris* (Cooper, 1863); *D. subramosus* MacFarland, 1966; *Diaulula sandiegensis* (Cooper, 1862); *Dirona albolineata* Cockerell & Eliot, 1905; *D. picta* Cockerell & Eliot, 1905; *Discodoris heathi* MacFarland, 1905; *Doridella steinbergae* (Lance, 1962); *Doriopsisilla albopunctata* (Cooper, 1863)
Eubranchius olivaceus (O'Donoghue, 1922); *E. rusticus* (Marcus 1961)
Fiona pinnata (Eschscholtz, 1831); *Flabellinopsis iodinea* (Cooper, 1862)
Hallaxa chani Gosliner & Williams, 1975; *Hermisenda crassicornis* (Eschscholtz, 1831); *Hopkinsia rosacea* MacFarland, 1905; *Hypsodoris californiensis* (Bergh, 1879)
Lacuna carinata Gould, 1848; *Laila cockerelli* MacFarland, 1905
Margarites helicinus (Phipps, 1774); *M. pupillus* (Gould, 1849); *Melibe leonina* (Gould, 1852)
Onchidoris bilamellata (Linnaeus, 1767); *O. muricata* (O. F. Müller, 1776)
Phidiana pugnax Lance, 1962; *Polycera atra* MacFarland, 1905;

P. hedgpethi Marcus, 1964; *P. zosteræ* O'Donoghue, 1924; *Precuthona divae* Marcus, 1961
Rostanga pulchra MacFarland, 1905
Spurilla chromosoma Cockerell & Eliot, 1905; *S. oliviae* (MacFarland, 1966)
Tenellia pallida (Alder & Hancock, 1854); *Tochuina tetraquetra* (Pallas, 1788); *Triopha carpenteri* (Stearns, 1873); *Triopha maculata* MacFarland, 1905; *Tritonia diomedea* Bergh, 1894; *Tritonia festiva* (Stearns, 1873)

Non-Mollusca

Adocia gelindra (de Laubenfels, 1932); *Aplysilla glacialis* (Dybowski, 1880)
Barentsia ramosa (Robertson, 1900); *Bugula californica* Robertson, 1905; *B. pacifica* Robertson, 1905
Didemnum carnulentum Ritter & Forsyth, 1917
Eurystomella bilabiata (Hincks, 1884)
Halichondria bowerbanki (Burton, 1930); *H. paniceum* (Pallas, 1766); *Hincksina velata* (Hincks, 1881); *Hymendesmia brepha* (de Laubenfels, 1930)
Lepas anatifera Linnaeus, 1758; *Lissodendoryx firma* (Lambe, 1895)
Metridium senile (Linnaeus, 1767)
Pachycerianthus fimbriatus (McMurrich, 1910); *Ptilosarcus gurneyi* (Gray, 1860)
Tubularia crocea (Agassiz, 1862)

found on the ascidian *Didemnum carnulentum* Ritter & Forsyth, 1917. The nudibranchs had grazed large portions of the ascidian.

Several very large (over 100mm) specimens of both *Diaulula sandiegensis* and *Archidoris montereyensis*, along with their nidosomes, have been collected on a sponge (tentatively identified as *Halichondria bowerbanki* Burton, 1930) in an erosion channel in the upper third of Elkhorn Slough, Monterey County, California. As in many of the above cases, depressions had been rasped into the sponge. Further, this was the only species of sponge noted to be present in the channel and hence, possibly the only available food.

Over a period of 3 years, large numbers of *Cumanotus beaumonti*, frequently with their nidosomes, have been observed on and collected from the gymnoblastoid hydroid *Tubularia crocea* (Agassiz, 1862). We have never found *C. beaumonti* on any substrate other than *T. crocea*, and if the nudibranch is removed from the hydroid, it immediately seeks to return to the hydroid. In the laboratory, the eolids were observed to feed upon the polyps of the hydroid.

On 12 April 1977, large numbers of the eolid *Phidiana pugnax* were found in close association with the gymnoblastoid hydroid *Hydractinia* sp. at Carmel Point, Monterey County, California. Later, in laboratory aquaria, the *Hydractinia* colonies were quickly consumed by *P. pugnax*. We have never observed them consuming other hyd-

roids, though they are known to attack other nudibranchs under crowded aquarium conditions (LANCE, 1962a).

Over a period of several years, small (3 to 7mm total length) specimens of *Onchidoris muricata* have been collected, almost always on the encrusting bryozoan *Reginella mucronata* (Canu & Bassler, 1923).

PREVIOUS FOOD RECORDS

Table 1 summarizes our search of the literature relevant to the recorded food habits of California nudibranchs. Included are the new data reported in this paper as well as additional personal observations of nudibranchs on possible food species which they were not actually seen to ingest (indicated by ^P). Where more than a single food item is listed, the order of listing does not imply preference (which is often unknown) of the nudibranch. We include the table as a guide to those who may find it useful in doing additional ecological or experimental studies of California nudibranchs.

DISCUSSION

The summary table includes certain nudibranch species from California that are also found in other geographical

areas (e.g., *Aeolidia papillosa*, *Acanthodoris pilosa*, *Onchidoris muricata*, *Dendronotus frondosus*, and others). Hence, the food items reported here may not necessarily be present in California. Widely distributed nudibranch species may well have additional food items or different preferences in different geographical locations. Certainly for *A. papillosa*, the studies of WATERS (1973) suggest that the major prey preferences differ between those occurring in Atlantic waters and those occurring in Pacific waters. Such differing prey preferences have not, to our knowledge, been investigated for other nudibranchs with wide geographical ranges. The whole field of prey preference studies for most California nudibranchs remains relatively little explored, and we hope this review may stimulate additional work.

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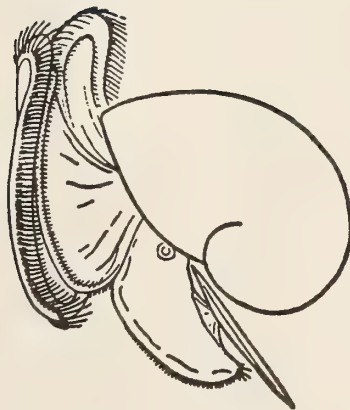
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Food Preferences, Food Availability and Food Resource Partitioning in Two Sympatric Species of Cephalaspidean Opisthobranchs

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(1 Text figure)

INTRODUCTION

EXTENSIVE STUDIES of the food resources and the feeding habits of cephalaspidean opisthobranchs are uncommon. With the exception of PAINE's (1963, 1965) studies of *Chelidonura* and BURN & BELL's (1974a, 1974b) work on 2 species of *Retusa*, most data concerning cephalaspidean feeding habits have been incidentally reported in papers documenting other aspects of their biology. Such reports indicate that cephalaspideans feed on a variety of epifaunal and infaunal organisms. HURST (1965) reported that *Philine aperta* (Linnaeus) had fed on Foraminifera and small gastropods and that *Scaphander lignarius* (Linnaeus) had ingested Foraminifera, young urchins, tectibranch gastropods, small bivalves and the polychaete *Pectinaria*. The guts of *Cylichna cylindracea* (Pennant) and *C. magna* Lemche were reported by LEMCHE (1956) to contain Foraminifera, as were the guts of *Retusa chrysoma* Burn and *R. pelyx* Burn by BURN & BELL (*opp. cit.*), *R. obtusa* (Montagu) by HURST (*op. cit.*) and *R. ovoidea* (Mil.), *R. truncatula* (Bruguière) and *R. variabilis* (Mil.) by BACESCU & CARAION (1956). Along with Foraminifera, small gastropods were also recorded among the gut contents of *R. truncatula* and *R. chrysoma*. HURST (*op. cit.*) and BURN & BELL (1974b) appear to be the only 2 papers reporting observation of foraminiferan ingestion by cephalaspideans.

As a result of extensive benthic sampling in Monterey Bay by the Moss Landing Marine Laboratories, a large

number of specimens of 2 co-occurring cephalaspidean opisthobranchs, *Acteocina culcitella* and *Cylichna attonsa* was available for study. Since these 2 species regularly co-occurred in the same habitats, shared similar anatomical characteristics and, in exploratory dissections, appeared both to feed upon Foraminifera, the present study was undertaken to analyze their food habits and to relate them to food availability. Specifically, we were interested in investigating how 2 such similar species could coexist and how they divided up the food resource.

MATERIALS AND METHODS

The specimens analyzed in this study were collected from 3 stations in northern Monterey Bay, California. The stations were designated as follows: Station 1105: lat. 36°51.0'N; long. 121°49.8'W; depth 16.5m; Station 1152: lat. 36°54.8'N; long. 122°01.0'W; depth 36.0m; Station 1177: lat. 36°53.6'N; long. 121°57.5'W; depth 34.5m. The locations are also shown on Figure 1. These stations were sampled at roughly 3-month intervals from August 1971 through November 1972.

The specimens were collected with a Smith-McIntyre grab which had a sampling area of 0.1 m² (SMITH & MCINTYRE, 1954). During the first sampling period (August 1971), 8 replicate samples were taken at each station. During the remaining sampling periods (November 1971, February, May, August, and November 1972), 6 replicates were taken at all the stations except 1105.

Each grab sample was sieved through 1 mm Nytex screens using filtered sea water. The specimens were relaxed with magnesium chloride (MgCl_2) and stained with rose bengal in order to differentiate living from dead specimens. Each sample was preserved in 10% buffered formalin and later transferred to 70% ethanol.

Specimens of *Acteocina culcitella* and *Cylichna attonsa* were individually dissected to analyze for any food remains in their digestive tracts. Because of the small size of the opisthobranchs, all examinations were performed under a dissecting microscope. Before dissection, all specimens of *A. culcitella* were measured for greatest shell length.

Using an ocular micrometer, Foraminifera obtained from the cephalaspidean digestive tracts were also measured.

In order to compare the Foraminifera ingested by the snails with the Foraminifera available in the sediment, the 3 stations were again sampled on 21 May 1974. As before, each station was sampled with the Smith-McIntyre grab using the same procedures described above. In addition, each station was also sampled using a Phleger

corer (3.6 cm inner diameter). In the laboratory, each core was kept vertical and then sliced into 1 cm sections which were stained with rose bengal and preserved with ethanol. In this way, the vertical distribution of living Foraminifera within the sediment could be determined. Each 1 cm subsample was thoroughly dried in an oven (65°C) and the Foraminifera were separated from the sediment by using a solution of bromoform (CHBr_3) in which the specific gravity had been adjusted to 2.2 by the addition of methanol. GIBSON & WALKER (1967) have shown that, at this density, bromoform is consistently more effective in separating Foraminifera from sediment particles than is carbon tetrachloride. Similar results were reported by SEN GUPTA (1971) who recovered 99% of the available Foraminifera with bromoform (diluted with acetone), but only 50 - 85% with carbon tetrachloride.

Overlap in food utilization between the 2 species was calculated using indices R_o , C_λ , derived from information theory as described by HORN (1966). Niche breadth was calculated from formulae of LEVINS (1968).

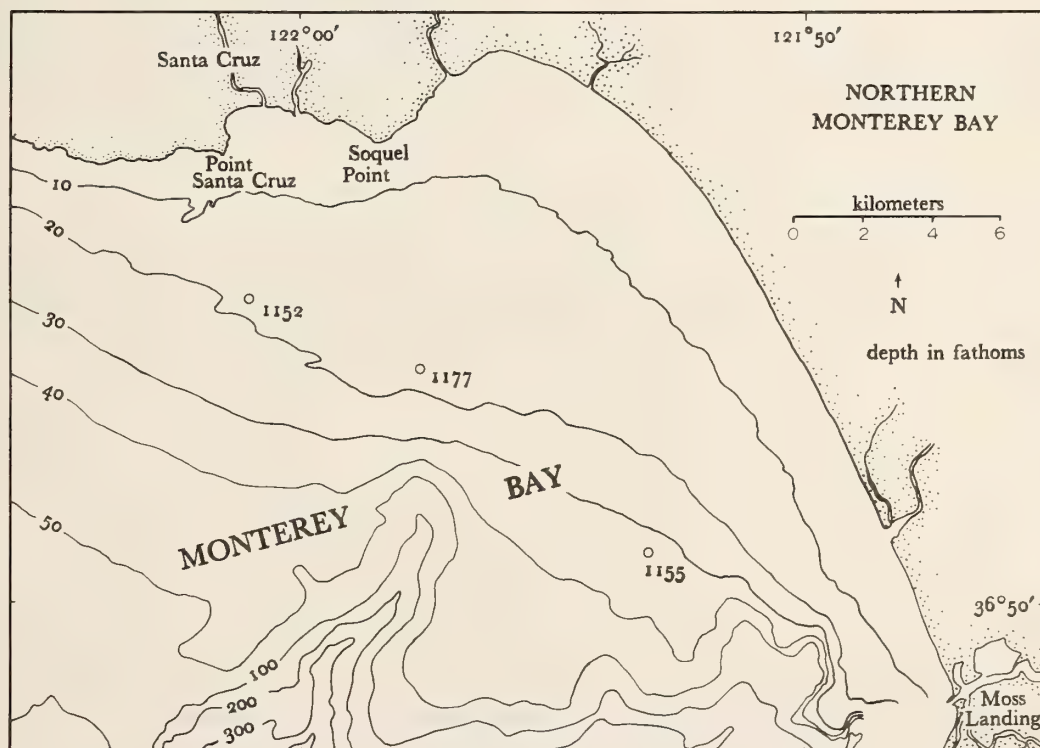


Figure 1

Map of Northern Monterey Bay, California
showing location of the three sampling stations

Number of Food items Recovered from Digestive Tracts of *Acteocina culcitella*[illegible]

fied as either *N. basispinata* (Cushman, Moyer) (50%) or as *N. stella* (Cushman, Moyer) (22%). The remaining 23% were too small for specific identification and are listed as *Nonionella* sp. These data are displayed in Table 2.

As with the rotaliids taken from *Acteocina culcitella*, those taken from *Cylichna attonsa* showed no obvious signs of chemical or physical damage, even when recovered from the gizzard or beyond. Of the 7 Foraminifera which were not *Nonionella*, 5 specimens were *Buccella frigida* (Cushman) and 2 were *Elphidiella hannah* (Cushman).

Food Availability

The abundance and vertical distribution of Foraminifera collected with the phleger corer were analyzed. These were compared with Foraminifera recovered from the digestive tracts of *Acteocina culcitella* and *Cylichna attonsa* taken at the same stations 1152, 1155, and 1177.

The vertical distribution of living Foraminifera within the top 4 cm of sediment at Stations 1152, 1155, and 1177

on 21 May 1974 is shown in Table 3. In all cases, only the Foraminifera from the top 4 cm are shown because Foraminifera decreased markedly below a depth of 4 cm and because our initial observations suggested that the 2 mollusks could not burrow below 4 cm. At stations 1155 and 1177, 97.1% and 93.1%, respectively, of all Foraminifera occurred within the first 4 cm, while at Station 1152, 77.7% are within the top 4 cm and 96.1% of all Foraminifera are found by the 5th centimeter. Within the first 4 cm, no distinct pattern of stratification could be discerned, either in the number of individuals or in species composition. The highest number of Foraminifera occurred within the 0-1 cm increment at Station 1155, the 2-3 cm increment at Station 1177 and the 3-4 cm increment at Station 1152. Similarly, the highest number of foraminiferal species occurred within the first cm of substrate at Stations 1155 and 1177, but within the 1-2 cm and the 3-4 cm increments at Station 1152. Certain species occurred at only one level (e.g., *Bolivina* sp., *Globobulimina pacifica* and *Nonionella fragilis*), while others (e.g., *Nonionella basispinata* and *Buliminella elegantissima*) occurred at all 4 levels.

Table 3

Distribution and Abundance of Foraminifera in the Top 4 cm of Substrate at 3 Stations

Species	Sta. 1152 (2 cores) Increment (cm)				Sta. 1155 (1 core) Increment (cm)				Sta. 1177 (2 cores) Increment (cm)				Total Per 4 cm		
	0-1	1-2	2-3	3-4	0-1	1-2	2-3	3-4	0-1	1-2	2-3	3-4	1152	1155	1177
<i>Haplophragmoides</i> sp.			0;2		8	4	1						2	13	0
<i>Textularia</i> sp.				1;1	1						1;1	1;0	2	1	3
<i>Trochammina inflata</i>				26;14					2;2		1;3		40	0	8
<i>Pelosina</i> sp.					6	4	5	5					0	20	0
<i>Protocornina</i> sp.					4			2					0	6	0
<i>Quinqueloculina</i> sp.	3;2	0;1		1;1		1	4		2;2		2;1		8	5	7
<i>Buccella frigida</i>		1;0			47	13	22	13	4;6				1	95	10
<i>Bolivina</i> sp.					1								0	1	0
<i>Buliminella elegantissima</i>		8;4	3;1						2;4	1;1	15;11	4;10	16	0	48
<i>Elphidella hannah</i>	1;1	1;1	2;2		3		3			7;8			8	6	15
<i>Globobulimina</i> sp.						1							0	1	0
<i>Nonionella basispinata</i>	1;1	3;4	5;11	1;3	20	5	11	7	0;1		8;3		29	43	12
<i>Nonionella fragilis</i>		7;12			3								19	3	0
<i>Nonionella globosa</i>			1;1	2;1									5	0	0
<i>Nonionella stella</i>		20;15	8;14	2;2	3	4	2			1;1		1;1	61	9	4
Total Per cm															
Core 1	5	40	14	32	96	32	48	27	10	8	27	6			
Core 2	4	37	31	22					15	9	19	11			
\bar{X} /Core	4.5	38.5	22.5	27					12.5	8.5	23	8.5			
Total Per 4 cm															
Core 1	91				203				51						
Core 2	94								54						

DISCUSSION

The diets of 2 sympatric cephalaspidean opisthobranchs are reported herein for the first time. Both are demonstrated to feed upon Foraminifera. MURRAY (1973) has suggested that Foraminifera may be ingested by 2 types of feeder, unselective predators who ingest sediment which contains Foraminifera, and selective predators who preferentially seek out Foraminifera.

Analyses of the food items recovered from the guts of both *Cylichna attonsa* and *Acteocina culcitella* suggest that neither can be placed in the category of unselective predators. The 2 species ingest different food items, even though the same food resources are available to both. *Cylichna attonsa* is extremely stenophagous and feeds only upon foraminiferans of the genus *Nonionella*. Foraminiferans of the genus *Nonionella* comprise from 3.3 to 23.6% of the individuals in the top 4 cm of the core samples from the 3 sampling stations, but in no case are they the most abundant foraminiferan in the sample. They are, however, second in abundance rank at Stations 1155 and 1152 and 4th at Station 1177. *Cylichna attonsa*, therefore, is a specialist concentrating upon one of the abundant foraminiferan genera. Such extreme stenophagy suggests that the abundance of *Nonionella* does not vary much over the course of the year. Unfortunately, we lack data on abundance of the foraminiferan fauna for other seasons of the year.

Acteocina culcitella, on the other hand, is more of a generalist, feeding upon 13 different species of Foraminifera as well as taking a few other small invertebrates. If *A. culcitella* were an unselective predator, it would be expected that the food items in the guts of the cephalaspidean would be in the same abundance as in the sub-

strate samples. A series of Spearman rank correlation tests comparing the abundance of the foraminiferans in the diet with those in the substrate were all insignificant ($P > 0.05$), indicating that at all 3 stations *A. culcitella* does not take food in relation to abundance. Hence, this species, although a generalist, is a selective predator.

The Foraminifera which were the highest in abundance in the guts of *Acteocina culcitella* were *Buccella frigida* and *Quinqueloculina* sp. In the top 4 cm of the substrate at the 3 stations, *B. frigida* was first in abundance only at Station 1155, whereas at Stations 1152 and 1177, it ranked 11th and 4th, respectively. *Quinqueloculina* sp. ranked 6th in abundance at Station 1152, 8th at Station 1155 and 6th at Station 1177. This is further evidence that *A. culcitella* does not take prey in relation to its abundance in the substrate.

To see whether *Acteocina culcitella* changed its diet with respect to season, we made tests comparing the rank abundance of prey items in the diet among the sampling dates for the 3 stations. In all cases, there were significant correlations in rank abundance of prey between any 2 sampling dates (Spearman rank test, $P < 0.05$, all comparisons). This suggests that either there is no difference in the composition of the prey over season, or that *A. culcitella* maintains its dietary preference in the face of changing abundances of prey organisms, since the significant rank correlation values mean that there is a very low probability that the 2 sets of values compared could have come from different populations.

Because the 2 opisthobranch species differ markedly in the prey species which they ingest, there is very little overlap in the diets of the 2; hence, the low values of the overlap index shown in Table 4. We conclude, then, that no significant competition occurs between these 2 species with respect to food.

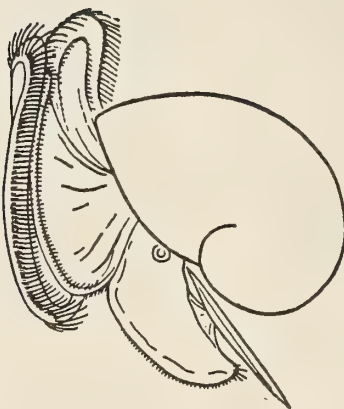
Table 4

Overlap Values for Diets of *Cylichna attonsa* and *Acteocina culcitella* at 3 Stations and Niche Breadth for *Acteocina culcitella*

Date	Station 1152			Station 1155			Station 1177		
	C _λ	R _o	1/B	C _λ	R _o	1/B	C _λ	R _o	1/B
Aug 1971							0	0	4.05
Nov 1971				0.028	0.091	2.01			
Feb 1972	0.036	0.095	4.64	0.072	0.249	4.43			
May 1972	0	0	2.58	0.019	0.119	2.27	0.245	0.497	2.53
Aug 1972	0.029	0.103	4.04	0.134	0.276	1.92	0.162	0.283	5.11
Nov 1972	0	0	2.78						
May 1974	0	0	3.53	0	0	1.93	0	0	1.34

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Checklist of Marine Mollusks at Coyote Point Park, San Francisco Bay, California

BY

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(1 Text figure)

INTRODUCTION

COYOTE POINT IS LOCATED in the city of San Mateo on the western shore of San Francisco Bay, California. Within its boundaries are 4 marine habitats: salt marsh, pilings and floating docks, rocky rubble and boulders, and sandy beach (Figure 1). The harbor on the east side of the point has been created by extensive dredging and filling.

Although the park offers one of the southernmost extensive rocky intertidal habitats in San Francisco Bay, it has been studied poorly. PACKARD (1918) mentioned species taken in oyster beds near Point San Mateo. Records of introduced species at the park are given by STÖHLER (1962), HANNA (1966), CARLTON (1969), and WICKSTEN (1976). There are no quantitative data for any of the marine mollusks despite their abundance, importance in the local food chain, and use in a sport fishery.

From 1970 to 1977, I maintained a list of marine mollusks at the park. Notes on their natural history and seasonal occurrence also were kept. This paper presents this information in hopes that it will stimulate research in this unusual protected area and assist workers in determining the distribution of mollusks in San Francisco Bay.

METHODS

During 1970 to 1977, collecting trips were made at least once in each season of the year. All areas were sampled from the highest tidal zone to the -2.0 foot [-0.6m] tide level except at the mud flats, where extreme softness of the mud prevented exploration below the +1.0 foot [0.3m] tide level. Animals also were collected by means of SCUBA diving and snorkeling off Peninsula Beach and in the harbor at depths to 5m. The dredge tailings near

the harbor were examined for empty shells. Specimens of all species are available for inspection in the collections of the Coyote Point Museum or in my personal collection. Additional specimens were donated to the California Academy of Sciences in San Francisco.

The list of species is arranged in phylogenetic order. A species is termed resident (R) if it has been taken during all seasons of the year for 3 or more continuous years. Casual species (C) are natives found only once or twice during the period of study. Accidental species (AC) are introduced species found alive only once during 1970 to 1977, or which have been reported alive at the park since 1960. Those species termed offshore (O) have been found cast ashore after storms or strong waves during at least 3 consecutive years, but have not been observed by me in the intertidal zone. Except for *Tegula funebris*, all the species known only from dead shells were obtained in the dredge tailings.

Native species (N) are those whose place of origin is the west coast of North America. I follow the report of CARLTON (1975) in determining which species have been introduced from the Atlantic Ocean (A) or the area around Japan and Korea (J).

RESULTS

Of the 36 species found at Coyote Point, 20 (56%) are native, 14 (39%) have been introduced from the Atlantic Ocean, and 2 (5%) have been introduced from the western Pacific Ocean. The Atlantic species probably were brought in with eastern oysters (*Crassostrea virginica*) which were farmed near Coyote Point until about 1920 (BARRETT, 1963).

The pyramidellid snail *Odostomia* sp. belongs to a group in which identification to species is difficult. Until

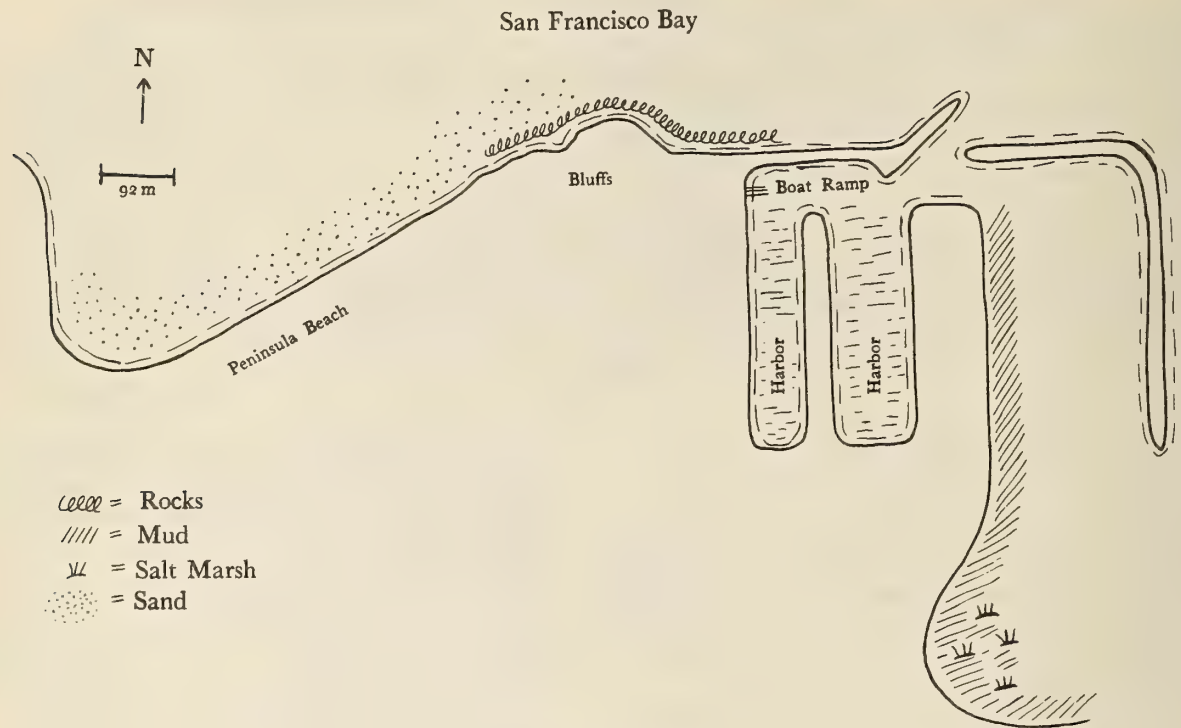


Figure 1

Map of Coyote Point

the species can be determined, its place of origin remains uncertain.

A flat slipper shell, *Crepidula perforans* (?) occurs only in apertures of large gastropod shells occupied by the hermit crab *Pagurus hirsutiusculus* Dana, 1851. Unlike *Crepidula nummaria*, this slipper shell lacks a shaggy periostracum and a deep shell. Although the Atlantic slipper shell *Crepidula plana* Say, 1822 may have been introduced into San Francisco Bay, I can detect no morphological differences between flat slipper shells from Coyote Point and shells taken from apertures of hermit crab-inhabited shells collected at Pacific Grove, off Santa Catalina Island, and along the Palos Verdes Peninsula, California. Until some means is found to distinguish *C. perforans* from *C. plana* in areas where the two might mingle, the identity of the flat slipper shell at Coyote Point remains uncertain.

Although 15 species of resident mollusks occur at Coyote Point, only 9 species were observed spawning or found as recently-settled individuals *Ilyanassa obsoleta*, *Urosal-*

pinx cinerea, and *Busycotypus* were observed laying egg masses during all seasons of the year. Two *Aplysia californica* produced egg masses in July, 1977. Egg-bearing *Crepidula convexa* and spawning *Mytilus edulis* were found during all seasons of the year. Very small, newly settled *Mytilus edulis*, *Tapes japonica*, and *Mya arenaria* were collected during summer months.

The turbid water of San Francisco Bay contains much plankton and detritus which can be used as food by the suspension feeders and deposit feeders at Coyote Point. Abundant growths of diatoms, *Ulva* sp., and other algae nourish the herbivores. *Urosalpinx cinerea* eats *Ostrea lurida*, and may prey on barnacles at the point. *Busycotypus canaliculatus* and *Ilyanassa obsoleta* readily will feed on dead fish.

There are few predators on mollusks at Coyote Point. No echinoderms were found during the period of study. Except for *Urosalpinx cinerea*, no carnivorous gastropod has been observed preying on other mollusks. The rock crabs, *Cancer productus* Randall, 1839 and *C. antennari-*

Table 1

Species List

Species	Residency	Origin	Notes
AMPHINEURA:			
<i>Mopalia hindsii</i> (Reeve, 1847)	C	N	2 animals found by bluffs, 6 April 1977.
PELECYPODA:			
<i>Mytilus edulis</i> Linnaeus, 1759	R	N	On rocks, docks, and pilings.
<i>Musculus senhousia</i> (Benson, 1842)	O	J	Probably lives on soft bottom.
<i>Ischadium demissum</i> (Dillwyn, 1817)	AC?	A	Edge of salt marsh, 1975 (M. Danielson, pers. comm.)
<i>Ostrea lurida</i> Carpenter, 1863	R	N	On rocks, docks, and pilings.
<i>Epilucina californica</i> (Conrad, 1837)	C	N	2 animals cast ashore, 22 April 1973.
<i>Tapes japonica</i> Deshayes, 1853	R	J	In sand and mud.
<i>Mercenaria mercenaria</i> (Linnaeus, 1758)	AC	A	Collected in 1968 (Carlton, 1969).
<i>Gemma gemma</i> (Totten, 1834)	R	A	In sand and mud.
<i>Cryptomya californica</i> (Conrad, 1837)	C	N	1 animal commensal with <i>Arenicola brasiliensis</i> Nonato, 1958; August 1973.
<i>Mya arenaria</i> Linnaeus, 1758	R	A	In sand and mud.
<i>Macoma balthica</i> Linnaeus, 1758	R	A	In mud.
<i>Macoma nasuta</i> (Conrad, 1837)	R	N	In mud.
<i>Lyonsia californica</i> Conrad, 1837	O	N	Probably lives in soft bottom.
GASTROPODA:			
<i>Collisella digitalis</i> (Rathke, 1833)	R	N	On boulders at high tide.
<i>Collisella strigatella</i> (Carpenter, 1864)	R	N	On boulders in middle intertidal zone.
<i>Collisella pelta</i> (Rathke, 1833)	C	N	1 animal found on boulders, 2 January 1974 and 1 found on boulder, 2 July 1977.
<i>Littorina scutulata</i> Gould, 1849	R	N	On rocks at high tide level.
<i>Crepidula convexa</i> Say, 1822	R	A	On shells and cobble, low tide level.
<i>Crepidula nummaria</i> Gould, 1846	C	N	1 animal found on rock at low tide, 1972.
<i>Crepidula perforans</i> Valenciennes, 1846(?)	R	N?	Inside shells occupied by hermit crabs.
<i>Nucella lamellosa</i> (Gmelin, 1792)	C	N	3 animals under ledge, 25 March 1972.
<i>Urosalpinx cinerea</i> Say, 1822	R	A	Among <i>Ostrea lurida</i> and on rocks.
<i>Busycotypus canaliculatus</i> (Linnaeus, 1758)	O	A	Rarely found intertidally on sand or mud, more common on soft subtidal bottoms.
<i>Ilyanassa obsoleta</i> (Say, 1822)	R	A	On mud flats and in salt marsh.
<i>Phytia myosotis</i> (Draparnaud, 1801)	R	A	Under drift at high tide in salt marsh.
<i>Aplysia californica</i> Cooper, 1863	C	N	3 large animals found near rocks by bluffs, 2 July 1977.

us Stimpson, 1856 probably eat some pelecypods. The black-tailed shrimp *Crangon nigricauda* Stimpson, 1856 eats *Gemma gemma*. The bat ray *Myliobatus californica* Gill, 1865 and the leopard shark *Triakis semifasciata* Girard, 1859 eat pelecypods inhabiting shallow sandy or muddy bottoms off the park.

DISCUSSION

Fluctuating conditions of temperature, salinity, and turbidity at Coyote Point may prevent many species of mollusks from becoming residents. Casual species which

occur widely on the coast outside of San Francisco Bay may drift in as planktonic larvae or be recruited from other parts of the Bay when environmental conditions are favorable for their survival.

Of the 2 accidental species, *Mercenaria mercenaria* probably no longer occurs at Coyote Point. No live specimens have been found since 1968 (CARLTON, 1969), and no living populations are known near San Mateo. *Ischadium demissum*, however, is widespread in southern San Francisco Bay and may extend its range into the salt marsh at the park.

Except for *Tegula funebris*, all the species known only from dead shells are inhabitants of sandy or muddy bot-

Table 2

Species Known Only from Dead Shells

PELECYPODA:	
<i>Anadara transversa</i> (Say, 1822)	A
<i>Argopecten irradians irradians</i> (Lamarck, 1819)	A
<i>Crassostrea virginica</i> (Gmelin, 1791)	A
<i>Clinocardium nuttalli</i> (Conrad, 1837)	N
<i>Tresus nuttalli</i> (Conrad, 1837)	N
<i>Petricola pholadiformis</i> Lamarck, 1818	A
<i>Barnea subtruncata</i> (Sowerby, 1834)	N
GASTROPODA:	
<i>Tegula funebris</i> (A. Adams, 1855)	N
<i>Odostomia</i> sp.	N?

toms. *Tegula funebris* is abundant outside the Bay and near its mouth, which suggests that it may be a casual visitor to rocky areas at the park.

Only old, chalky valves of *Clinocardium nuttalli* and *Barnea subtruncata* were found in dredge tailings. However, entire shells of *Tresus nuttalli* were discovered buried with the gaping posterior end oriented toward the surface of the mud. PACKARD (1918) reported finding shells of *T. nuttalli* (as *Schizothaerus nuttalli*) and live individuals of *C. nuttalli* (as *Cardium corbis*) in southern San Francisco Bay. That these shells were found only in dredge tailings which also contain shells of *Crassostrea virginica* suggests that these native species occurred near the point in the

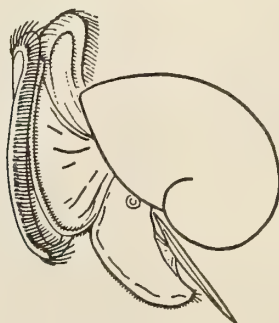
early part of the twentieth century. It is possible that these pelecypods were killed by dredging that buried them.

ACKNOWLEDGMENTS

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Infection of *Ostrea lurida* and *Mytilus edulis*
by the Parasitic Copepod *Mytilicola orientalis*
in San Francisco Bay, California

BY

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INTRODUCTION

Mytilicola orientalis is an endoparasitic copepod which infects the intestine and rectum of several bivalve species. Originally described from *Mytilus crassitesta* and *Crassostrea gigas* collected in the Inland Sea of Japan (MORI, 1935), it has been introduced to the Pacific coast of Canada and the United States, probably with the importation of Japanese *C. gigas*. Distribution is sporadic and limited to the immediate vicinity where infested oyster stock has been introduced (BERNARD, 1969). The parasite has been found in Washington waters in *Ostrea lurida*, *C. gigas*, *Mytilus edulis*, *Paphia* (= *Protothaca*) *staminea*, and *Crepidula fornicata* (ODLAUG, 1946). CHEW *et al.* (1964a) recorded infestation of *O. lurida*, *M. edulis*, and *M. californianus* from Humboldt Bay, California, and KATKANSKY *et al.* (1967) reported *C. gigas* infections in Yaquina Bay, Oregon. There are no previous studies dealing with *Mytilicola orientalis* infection of bivalves from the central California coast, particularly San Francisco Bay.

In British Columbia, *Mytilicola orientalis* has a single reproductive period from June to late August (BERNARD, 1969), while in California and Oregon there is continuous reproductive activity, although the numbers of females carrying egg sacs decrease during the winter (CHEW *et al.*, 1964b). SPARKS (1962) indicated that reproductive activity in Washington waters occurred only in fall and spring. Sparks also found peaks of *Crassostrea gigas* infection in the spring and fall, followed by rapid declines in infection rates. KATKANSKY *et al.* (1967) observed that the incidence and intensity of the copepod infections in *Ostrea lurida* did not vary significantly during the year and that there were no short-term cyclic occurrences of these parameters. There has been no previous work relating incidence or intensity, or both, of *Mytilicola* infections to host size.

In this study, *Ostrea lurida* and *Mytilus edulis* from San Francisco Bay were examined for the presence of *Mytilicola orientalis*. Rates of infestation were determined, as were seasonal fluctuations of mussel infections and copepod reproduction.

METHODS

The samples of both *Ostrea lurida* and *Mytilus edulis* were taken from an intertidal strip of rocky landfill at the Berkeley Marina, Berkeley, California. The oyster population was scattered in the much more dense population of mussels which covers nearly all the hard substrate present in the area. Between June, 1975 and June, 1976, 30 *O. lurida* were randomly sampled on a monthly basis, with the exception of 4 months when slightly fewer were taken. Mussels were sampled quarterly, commencing in the fall of 1975. These samples contained a minimum of 70 individuals. All samples of both bivalve species were taken from a similar tidal height (approximately the +0.3m level) to minimize variability in exposure to infection.

Before dissection, mussel lengths were measured to the nearest millimeter. Oyster lengths were not recorded, due to the great variability in the shape of oyster shells. Because of this variability, the length of the *Ostrea lurida* shell does not correlate either to size or weight of the oyster meat. All animals were examined under a dissecting microscope while fresh. The entire gut was opened and all *Mytilicola orientalis* removed and examined for visible egg cases. The incidence of infection is defined as the percent of the sample infected with *M. orientalis* while intensity of infection refers to the average number of parasites per infected host in the sample. There were 2 size classes of *M. orientalis* present in the bivalves, as noted by CHEW *et al.* (1964a), larger females 6 - 11 mm

in length, and males and immature females 2.5 mm in length.

RESULTS

The parasitic copepod *Mytilicola orientalis* was found in both *Ostrea lurida* and *Mytilus edulis* in San Francisco Bay. The incidence of infection was much greater in the

mussels at the study site, although ample oyster hosts were available. The rates of infection are compared in Table 1. Due to the low incidence of infection in *O. lurida*, we were unable to quantitatively examine the effect of the infection on either the host or the parasite.

Several aspects of the host-parasite relationship were investigated in the *Mytilus edulis* sampled. We found that in 3 of the 4 samples there was no correlation between the size of the host and the intensity of the infection. The single exception, that of the winter sample, indicated that larger *M. edulis* harbored fewer parasites per infected host ($P < 0.005$, using a linear regression analysis).

Of the data in Table 2, only the summer sample showed significant ($P < 0.005$) variation between the number of observed and expected infections of mussels, the smallest mussels being less infected than expected and the larger ones having higher than expected incidence. Table 2 indicates that throughout the year the highest rate of infection is present in medium-sized animals. Seasonal fluctuation of the incidence of infection was not significant in comparisons between any 2 seasonal samples, and the intensity of infection was not notably varied (Table 1).

The Arcsin Conversion Test (SOKAL & ROLF, 1969) was used to detect seasonal variation in *Mytilicola orientalis* reproductive activity. Females with egg sacs were found throughout the year at the study site, evidence that

Table 1

Incidence and intensity of *Mytilicola orientalis* infections in *Mytilus edulis* (quarterly samples) and *Ostrea lurida* (quarterly totals of monthly samples).

	# individuals in samples	Incidence (%)	Intensity (#/infected animal)
<i>Mytilus edulis</i>			
fall	101	40.6	2.1
winter	101	48.5	3.3
spring	70	37.1	2.6
summer	95	36.8	2.3
<i>Ostrea lurida</i>			
fall	90	0.0	0.0
winter	90	0.0	0.0
spring	103	1.0	2.0
summer	75	2.7	2.0

Table 2

Incidence of *Mytilicola orientalis* infection in *Mytilus edulis* by size class. Numbers of observed infections are by actual count. The numbers of expected infections were calculated according to the method of Sokal and Rolf (1969).

Size Class	Infected			Non-infected		
	%	Observed	Expected	%	Observed	Expected
<i>Mytilus edulis</i>						
length in cm						
0.0-2.5 fall	31	5	6	69	11	10
winter	23	5	11	77	17	11
spring	29	2	3	71	5	4
summer	12	3	9	88	21	13
2.6-4.5 fall	51	26	20	49	25	31
winter	57	39	34	43	29	34
spring	43	22	19	57	29	32
summer	45	20	7	55	24	15
4.6-8.0 fall	29	10	14	71	24	20
winter	45	5	6	55	6	6
spring	18	2	4	82	9	7
summer	44	12	4	56	15	9

the copepod reproduces continuously there. There was significant seasonal fluctuation in the occurrence of females carrying egg cases. The summer sample contained the greatest percentage of gravid females (31.8%), while the fall value of 5.9% was significantly lower ($P < 0.005$). There was significant ($P < 0.05$) difference between the winter value of 17.5% and the fall value. The difference between the winter and spring values was not significant, nor was that between the spring and summer, though the difference between the winter and summer values was significant ($P < 0.05$) (Table 3).

Table 3

Mytilicola orientalis reproductivity in *Mytilus edulis*.

	male/immature	female without eggs	female with eggs	% <i>M. orientalis</i> with eggs
fall	32	48	5	5.9
winter	99	33	28	17.5
spring	46	9	16	22.5
summer	45	13	27	31.8

DISCUSSION

The occurrence of *Mytilicola orientalis* in *Ostrea lurida* and *Mytilus edulis* is not surprising, as they were probably introduced when *Crassostrea gigas* was imported from Japan and cultured in south San Francisco Bay by the Consolidated Oyster Co. in the 1930's.

The present study site at the Berkeley Marina is approximately 24 km from the area where Consolidated Oyster Co. maintained its beds, indicating that *Mytilicola orientalis* has probably spread throughout San Francisco Bay in the last 40 years. There are no other reports on the presence of the copepod in San Francisco Bay bivalves, but a widespread distribution is likely. The fact that *Mytilus edulis* infections are more common than those in *Ostrea lurida* agrees with the reports of ODLAUG (1946) and CHEW *et al.* (1964b). Odlaug reported infections in *O. lurida* ranging from 1.0% to 9.2% and between 42.5% and 73.6% for *M. edulis* from Puget Sound. Chew *et al.* reported a 9.6% *O. lurida* infection rate and a 58.3% rate for *M. edulis* collected in Humboldt Bay, California. Since the *O. lurida* appeared to be randomly

mixed with and at the same tidal height as the *M. edulis* at our study site, the large difference in *M. orientalis* incidence might indicate a preferential infection of *M. edulis* by the copepod. HEPPER (1955) found that *Mytilicola intestinalis* is able to infect *Ostrea edulis* when the oysters are exposed to copepodites, but when *O. edulis* and *M. edulis* are both exposed to the infective stage in the same aquarium, the mussels are readily infected and oysters are not. CHENG (1967) also noted that it would appear that *M. intestinalis* demonstrated a preference for *M. edulis*, but if the mussel was not available for *M. intestinalis* copepodites to infect, they would parasitize *O. edulis* instead.

Since only one of our 4 *Mytilus edulis* samples showed a correlation between host size and intensity of infection, the present results disagree with those of GRAINGER (1961) and DAVEY & GEE (1976) for *Mytilicola intestinalis*, although BOLSTER (1954) found that differences in intensity of *M. intestinalis* infections may be slight, if there are any at all. At present, it is not possible to reconcile these reported differences.

The incidence of *Mytilicola orientalis* infections does not seem to occur more readily among a particular size class or classes of *Mytilus edulis*. As noted above, significant variation was found only in the mussels taken in the summer. This sample was taken in late summer and small mussels less than 2.5 cm in length were only a few months old (GRAINGER, 1961). The rapid growth of young mussels may have allowed the young mussels to reach several centimeters in length in a time sufficiently short such that infections are not established. Lack of significant seasonal fluctuation in incidence or intensity of infection in the *M. edulis* population studied agrees with the data of KATKANSKY *et al.* (1967), though seasonal fluctuation within a given size class is possible.

The presence of gravid female *Mytilicola orientalis* throughout the year, with a peak of activity in the summer, concurs with the report of CHEW *et al.* (1964b) for California and Oregon, rather than with BERNARD (1969) for British Columbia. The decrease of females carrying egg cases in the fall and the return to a higher winter value are unlike previous reports and were unexpected in view of the report by BOLSTER (1954) who indicated that low water temperatures reduced breeding efficiency in *M. orientalis*. The year-round reproductive activity of *M. orientalis* may be a result of hydrographic conditions in San Francisco Bay, but similar data are not available from other geographic regions with which to directly compare our data.

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Aestivating Giant African Snail Population in South Andaman During 1973, 1974, and 1975

BY

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Achatina fulica Bowdich, 1882 is a serious land snail pest of a number of vegetables, fruits, plantation crops, and ornamentals. During unfavourable weather conditions they undergo aestivation and on the return of favourable conditions they resume activity. The present work relates to the aestivating snail population. Work on such studies was initiated in 1969 in certain villages of South Andaman and the municipal area of Port Blair. An account of the aestivating giant African snail population during 1973 in 11 villages of South Andaman already has been published (ABBAS & GAUTAM, 1975). The present paper gives a comparative account of the aestivating snail populations in these villages during the summer seasons (January to April) of 1973, 1974 and 1975 (Table 1).

The present studies indicate that the position of 6 villages, namely Makkapahar, Calicut, Brishganj, Garacharma, Pahargaon and Dollyganj remained unchanged during these 3 years, while in the case of the other 5 villages there was a slight change. However, the trend in all the villages in all 3 years was of a decline of aestivating snail populations. At Makkapahar the aestivating snail population throughout these 3 years continued to remain highest, varying from 102.39 to 86.81/m², followed by Calicut, varying from 86.40 to 65.99/m². The villages nearer to the town of Port Blair had comparatively much lower snail populations (*i. e.*, Dolliganj, Nayagaon, Shadipur, Schoolline and Pahargaon); these 5 villages are only about 5 - 8 km from Port Blair, whereas Makkapahar and Calicut which stand I and II, respectively, are about 20 and 14 km distant. A similar trend was observed by ABBAS & GAUTAM in their 1973 studies on the aestivating giant

African snail population in these 11 villages. This trend now stands confirmed as a result of 3 years' continuous observations in these 11 villages.

SUMMARY

A comparative study of the aestivating population of the giant African snail in 11 villages of South Andaman was done during 1973, 1974 and 1975.

The highest average population per square metre was found to be 102.39, 98.54 and 86.81 respectively in 1973, 1974 and 1975 whereas the lowest population per square metre in the same years was found to be 20.10, 17.11 and 14.57 respectively.

It was observed that the population declined from year to year in all 11 villages. Villages nearer to Port Blair had the lowest population, whereas those farther away had the highest.

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Table I

Aestivating Giant African Snail Population in South Andamans in 1973, 1974 and 1975

Sl. No.	Locality	Data on aestivating pockets			Average population of snail/m ² and position of population			Remarks
		1973	1974	1975	1973	1974	1975	
1.	Schoolline	A. 34 B. 92.64 C. 2429	A. 50 B. 74.13 C. 1682	A. 143 B. 200.10 C. 3672	26.21/VIII	22.68/VIII	18.35/IX	
2.	Pahargaon	A. 68 B. 120.53 C. 3810	A. 67 B. 104.49 C. 2898	A. 226 B. 233.17 C. 6202	31.61/VII	27.73/VII	26.59/VII	Position unchanged
3.	Austinabad	A. 62 B. 106.76 C. 5567	A. 59 B. 54.39 C. 2371	A. 207 B. 268.55 C. 8845	52.14/IV	43.59/III	32.92/IV	
4.	Prothrapur	A. 75 B. 93.76 C. 5044	A. 53 B. 44.61 C. 1877	A. 148 B. 161.80 C. 6115	53.79/III	42.07/IV	37.71/III	
5.	Brischganj	A. 70 B. 99.99 C. 5079	A. 51 B. 42.91 C. 1713	A. 115 B. 115.37 C. 3483	50.79/V	39.92/V	30.19/V	Position unchanged
6.	Garacharama	A. 75 B. 91.53 C. 3163	A. 72 B. 71.46 C. 2143	A. 308 B. 259.28 C. 7289	34.55/VI	29.98/VI	28.11/VI	Position unchanged
7.	Calicut	A. 103 B. 119.97 C. 10366	A. 130 B. 73.49 C. 5818	A. 535 B. 340.23 C. 22452	86.40/II	79.16/II	65.99/II	Position unchanged
8.	Dollyganj	A. 52 B. 73.69 C. 1482	A. 41 B. 40.25 C. 689	A. 64 B. 57.16 C. 833	20.10/XI	17.11/XI	14.57/XI	Position unchanged
9.	Makkapahar	A. 81 B. 99.80 C. 10219	A. 102 B. 58.90 C. 5804	A. 536 B. 438.77 C. 38093	102.39/I	98.54/I	86.81/I	Position unchanged
10.	Shadipur	A. 57 B. 84.93 C. 2129	A. 52 B. 52.90 C. 1156	A. 240 B. 309.52 C. 6134	25.06/X	22.15/IX	19.81/VIII	
11.	Nayagaon	A. 60 B. 85.49 C. 2181	A. 49 B. 50.53 C. 1043	A. 169 B. 160.53 C. 2802	25.61/IX	20.64/X	17.45/X	

A. = Number of aestivating pockets.

B. = Area of aestivating pockets.

C. = Number of aestivating Snails.

Temporal Changes in a Tropical Rocky Shore Snail Community

BY

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(1 Text figure)

INTRODUCTION

MORE SPECIES ARE GENERALLY found in tropical communities than in comparable temperate communities, and rocky shore gastropod assemblages are no exception. On Pacific Ocean rocky shores, the same collecting effort will yield about 2.4 times as many species in Costa Rica as in Oregon (MILLER, 1974). Rocky shores contain the same range of habitats at both latitudes (SPIGHT, 1977). If the average tropical snail uses fewer habitats than a typical temperate one, the tropical species would be more specialized, but overlap among species could be about the same as in temperate waters. Alternatively, tropical snails can utilize the same range of habitats as their temperate counterparts; when this is the case, overlap among species will be much greater than in temperate communities.

To determine whether tropical snails use fewer habitat types than temperate ones do, I collected snails from a number of quadrats at Playas del Cocos, in northwestern Costa Rica during 1970 (SPIGHT, 1976). Each quadrat was characterized by its shore level, substrate, and degree of wave exposure. Using these variables, habitat descriptions were constructed for all species. Most Costa Rican snails use fewer of these habitat types than do typical snails from Washington State (*i. e.*, they are more specialized; SPIGHT, 1977).

Habitat descriptions tell where snails were found, but not how often they were found where they were supposed to be. Tropical snails were found less often on patches of "suitable habitat" (places included in their habitat description) than temperate ones were (SPIGHT, 1977). Many of these "absences" may have been observed because habitat descriptions were not precise enough (*e. g.*, the investigator did not recognize as many habitat types as the

snails do). On the other hand, tropical snails may simply be less predictable than temperate ones.

One can assess predictability by observing how distributions change over time. To assess year-to-year distributional changes, I returned to Playas del Coco in 1971 and resampled 2 quadrats I had examined during 1970. Two questions were asked: 1) are the assemblages at one place similar in successive years, and 2) can year-to-year changes at one place be accounted for by growth of residents and recruitment of juveniles? The discussion will examine the results in terms of habitat selection and other factors causing distributional patterns.

METHODS

The quadrats are more or less uniform areas of rock reef, sufficiently differentiated from the surrounding areas to be readily recognized without artificial markers. The quadrat exposed to moderate wave action (Q-11) is a flat 6m² portion of a highly dissected rock face on the north side of Punta Miga (height, 0.67m above mean low water [MLLW]). The calm-water quadrat (Q-8) is a 3m² area on the extreme southern portion of Bahía El Coco (height 1.4m above MLLW). It is protected from oceanic conditions by Punta Miga. Most of the reef near Q-8 is buried by silty sand, but the reef is continuously exposed about 1m further along the beach (see SPIGHT, 1976, for maps showing quadrat locations and for further sampling details).

On each visit (8 February - 21 March, 1970; 7-14 February, 1971), all gastropods were handpicked from the quadrats. The snails were sorted to species, and all those larger than 6mm were measured with vernier calipers. Individuals that could be readily identified were re-

Table 1

Comparison of gastropod assemblages found in different years on two rocky-shore quadrats at Playas del Coco, Costa Rica.

Species	Collection of 1970				Collection of 1971			
	N	Shell length (mm)			N	Shell length (mm)		
		Range	Mean	SD		Range	Mean	SD
Quadrat with moderate wave action (Q-11)								
<i>Acanthina brevidentata</i> (Wood, 1828)	47	13-22	16.0	1.52	46	8-20	14.0	3.14
<i>Thais melones</i> (Duclos, 1832)	26	12-37	21.2	5.99	34	13-40	21.0	7.55
<i>Fissurella virescens</i> Sowerby, 1835	33 ¹	21-42	30.1	5.49	87 ²	—	—	—
<i>Siphonaria maura</i> Sowerby, 1835	5 ³	10-18	15.0	3.00	14	9-20	14.7	3.24
<i>Fissurella longifissa</i> Sowerby, 1863	51 ³	19-23	20.8	1.64	+ ²	—	—	—
<i>Opeatostoma pseudodon</i> (Burrow, 1815)	0	—	—	—	4	9-22	17.0	5.60
<i>Anachis lentiginosa</i> (Hinds, 1844)	0	—	—	—	2	7-8	7.5	—
<i>Thais speciosa</i> (Valenciennes, 1832)	1	9	9.0	—	0	—	—	—
<i>Siphonaria gigas</i> Sowerby, 1825	1 ³	15	15.0	—	0	—	—	—
<i>Scurria stipulata</i> (Reeve, 1855)	0	—	—	—	1	20	20.0	—
Quadrat in calm-water area (Q-8)								
<i>Acanthina brevidentata</i> (Wood, 1828)	188	6-26	9.9	1.94	252	6-24	17.0	4.16
<i>Anachis costellata</i> (Broderip and Sowerby, 1829)	246	5-18	13.6	2.71	105	6-19	13.4	3.71
<i>Anachis lentiginosa</i> (Hinds, 1844)	69 ³	3-6	—	—	127	—	—	—
<i>Anachis rugulosa</i> (Sowerby, 1844)	133 ³	3-6	—	—	134	—	—	—
<i>Nerita funiculata</i> Menke, 1851	92	3-13	7.5	2.20	45	3-12	8.4	2.24
<i>Thais biserialis</i> (Blainville, 1832)	53	4-24	12.3	4.87	76	5-38	13.7	7.77
<i>Fossarius</i> sp.	12 ³	3-5	—	—	14	—	—	—
<i>Anachis pygmaea</i> (Sowerby, 1832)	6	6	—	—	6	—	—	—
<i>Notoacmea biradiata</i> (Reeve, 1855)	8 ³	6-11	8.9	1.73	0	—	—	—
<i>Purpura pansa</i> Gould, 1853	1	32	32.0	—	0	—	—	—

¹Collected from only 1 m × 2 m portion of quadrat; all others are numbers for entire 2 m × 3 m quadrat (Moderate wave action) or entire 1.5 m × 2 m quadrat (Calm-water).

²Fissurellids were counted (on entire quadrat) but not measured in 1971, and the species were not separated; both species were present.

³All specimens collected in 1970 were removed permanently from the quadrat; for other species all but a few voucher specimens were returned to the quadrat within a few days after collection.

turned to the quadrat within 24 hours; other individuals were preserved for later study.

Some Q-11 snails were tagged to obtain growth rates. On 8 February 1970, 66 *Thais melones* (Duclos, 1832), 30 *Acanthina brevidentata* (Wood, 1828) and 10 *Opeatostoma pseudodon* (Burrow, 1815) were given individually numbered tags and returned to Q-11. When the complete collection was made (8 March 1970), 23 of these snails were recaptured, and on 21 March, 11 additional tagged snails were captured. No tagged snails were found in 1971.

To evaluate the growth data, the observed increments of shell length were regressed on initial size. Of the 3 regressions, only that for *Acanthina* over the 8 February-8 March interval was significant ($F_{1,8}=4.15$; $0.10 > P > 0.05$). Since growth was poorly correlated with size, the data are presented here as unweighted averages.

RESULTS

The collections made in 1971 are much more similar to those taken from the same quadrats in 1970 (Table 1) than to collections from other quadrats (SPIGHT, 1976). For most species, both density and mean shell length were similar in 1970 and 1971. Furthermore, most of the individuals kept for vouchers after the 1970 collection had been replaced by others of the same species by 1971.

Species lists for the 2 years are not identical. Of the 18 species collected, 4 were found only in 1970, and 3 were found only in 1971 (Table 1). However, of these 7 species only *Notoacmea biradiata* was represented by as many as 8 individuals (1970; these were preserved).

Densities and size distributions also changed between years (Figure 1). Along with limited growth data, these size distributions reveal the underlying processes that

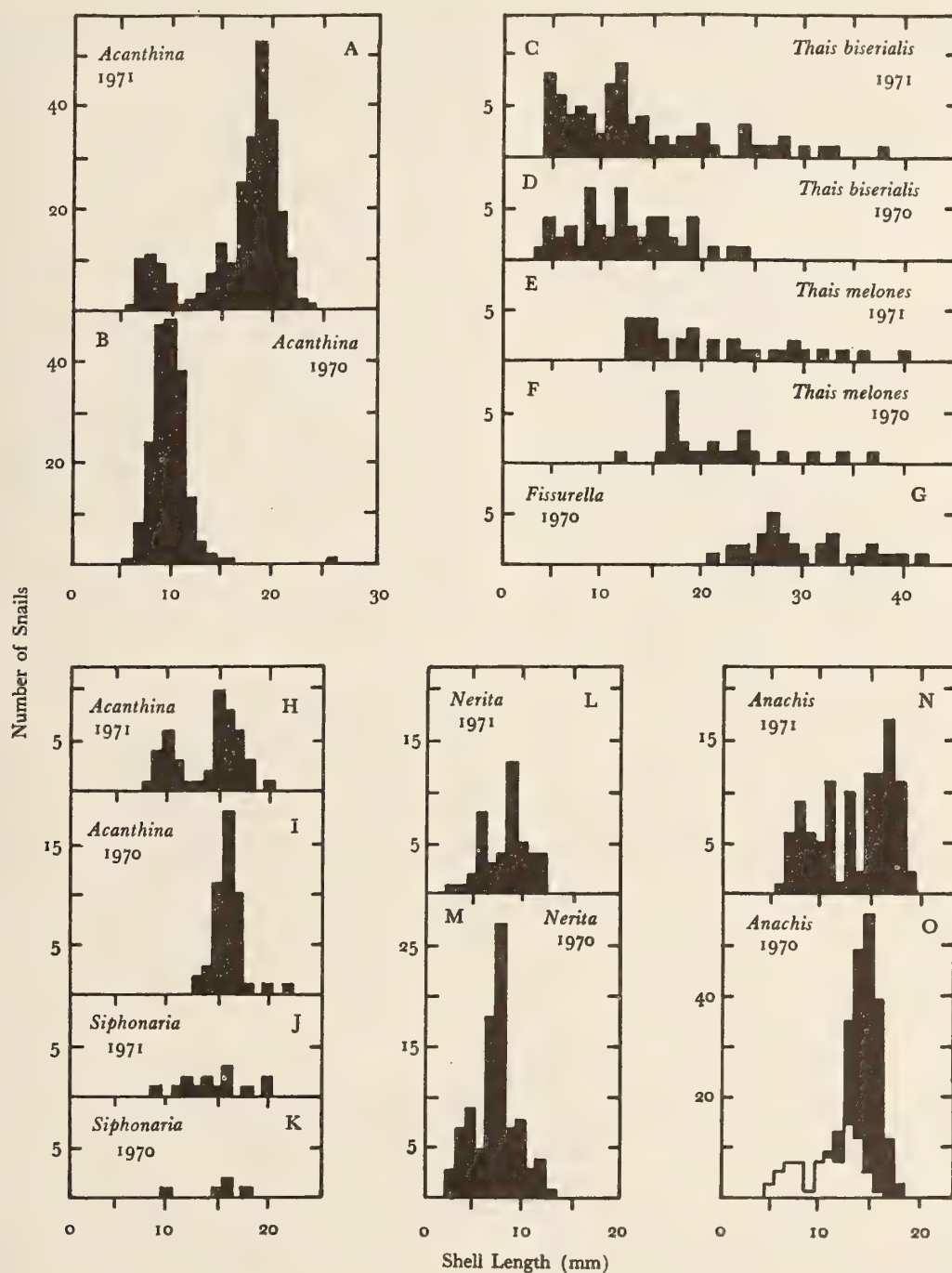


Figure 1

Sizes of snails collected from Q-8 and Q-11 during 1970 and 1971. *Acanthina brevidentata* (A, B), *Thais biserialis* (C, D), *Nerita funiculata* (L, M), and *Anachis costellata* (N, O) were collected from Q-8, while *Thais melones* (E, F), *Fissurella virescens* (G),

Acanthina brevidentata (H, I), and *Siphonaria maura* (J, K), were collected from Q-11. Note that the vertical scales for A, B, and O are twice those for all other figures. The white columns on O refer to snails with thin lips, and the dark columns to snails with thick lips.

maintain the composition of these gastropod assemblages. The data will be reviewed for each of the major species in turn.

Acanthina brevidentata — The size distributions have definite peaks (Figure 1-A, B, H, I), and these probably correspond to year classes. The first peak is at about 10 mm, which is at the lower end of the yearling size range for typical temperate *Thais* (*T. emarginata* (Deshayes, 1839), *T. lamellosa* (Gmelin, 1791) and *T. lapillus* (Linnaeus, 1758) (SPIGHT, 1975). The second peaks are at about 16 mm and 19 mm, the latter typical for second-year *T. emarginata* and *T. lapillus* (SPIGHT, 1972; FEARE, 1970a). However, 8 - 10 mm annual increments would require more rapid growth than that actually measured during the February-March period of 1970 (Table 2).

Known spawning times are consistent with these age assignments. *Acanthina* deposited eggs on Q-8 during February, 1971, and elsewhere during March, 1970. If most snails spawn during February and March, then the smaller size peak (Figure 1) would represent snails almost exactly 1 year old. However, temperate muricids that attain only 20 - 25 mm as adults spawn more than once (*Thais lapillus*, FEARE, 1970b) and frequently repeatedly throughout the year (*T. emarginata*, HOUSTON, 1971; *Eupleura caudata* (Say, 1822), MACKENZIE, 1961). *Acanthina* may also have a long spawning season.

The size distributions (Figure 1) indicate that many more recruits settled at some times and places than others. The size distribution for each quadrat is unimodal in one collection and bimodal in the other. In 1970, the Q-8 population consisted entirely of yearlings, and the Q-11 population entirely of adults. Yearlings

were present on both quadrats in 1971, but fewer were found on Q-8 than had been found in 1970. Thus, during 1969 many snails recruited to Q-8, while only a few recruited to nearby Q-11.

The estimated annual growth performances and the observed dry-season growth rates are lower than typical temperate ones. Snails grow slowly when food is sparse (SPIGHT, 1972) and food supplies appeared to be sparse at Playas del Coco. The major prey of *Acanthina* is *Chthamalus* (PAINE, 1966). The most common species at Playas del Coco, *C. panamensis*, is small and was sparse on both visits. Both barnacles and mussels were more abundant on Q-8 than on Q-11, and, appropriately, snails grew faster and reached larger sizes on Q-8.

The Q-8 is a sandy area, and sand levels shifted during the observation period. At times the entire Q-8 area is probably submerged by the sand. The *Acanthina brevidentata* on this quadrat were unusually numerous, and many more juveniles were found here than elsewhere. The size distributions may indicate recolonization after a recent burial.

Thais melones — The size distributions and growth data indicate growth rates similar to those of *Acanthina*. Most snails found were 15 - 25 mm (Figure 1-E, F) and these are assumed to be second year juveniles. Since the second-year snails of 1971 are not represented as first-year snails in 1970, the actual annual growth performances are not clear. If snails settled after the 1970 visit, they must have reached 15 - 25 mm in 10 months or less. However, the tagged snails grew much more slowly. Alternatively, the snails settled before the 1970 visit and I failed to observe them. Since the crevices on the quadrat

Table 2

Net growth by three Costa Rican snails during the 1970 dry season.

Species	N	Size Range (mm)	Net Size Increase (mm)		SD	r
			Maximum	Mean		
8 February to 8 March						
<i>Thais melones</i>	13	12-36	1.0	0.49	0.29	0.094
<i>Acanthina brevidentata</i>	10	11-22	1.6	0.21	0.50	-0.584
8 February to 21 March						
<i>Thais melones</i>	9 ⁴	15-29	2.6	0.80	0.84	-0.240
<i>Acanthina brevidentata</i>	2 ⁵	15-16	0.5	0.45	—	—
<i>Opeatostoma pseudodon</i>	1	17	2.6	2.6	—	—

r, correlation between initial size and net size increase

⁴includes one of the snails recaptured 8 March

⁵neither snail recaptured 8 March

could provide hiding places for most snails 4 - 6 mm long, the 15 - 25 mm snails of 1971 could have settled as early as October or November, 1969. Assuming that fall is the normal settlement period, the year classes of 1968 and 1969 were about equally large, and the 1968 snails grew slightly faster than the 1969 ones.

The *Thais melones* size range is similar to that of *T. lamellosa* (SPIGHT, 1974), and therefore a similar mature size of 25 - 35 mm can be expected for Playas del Coco snails.

Thais biserialis — The size distributions do not have discrete peaks (Figure 1-C, D), and therefore growth rates cannot be derived. Most snails were 4 - 20 mm, and these were probably first and second year juveniles. The continuous size distribution suggests continuous recruitment, in contrast to *Acanthina*. The size range should correspond to an adult size greater than 25 mm (which is unusually large for a species that breeds throughout the year; SPIGHT *et al.*, 1974). No adults were present in 1970, and only a few were found in 1971. If the 1971 adults were among the juveniles collected in 1970, then each must have grown about 10 mm during the year. The dense population of juveniles may indicate a recent colonization of Q-8.

Anachis costellata — Shell morphology may indicate maturity, allowing snails to be aged. In 1970, the smaller snails had thin lips and rounded shoulders, while the larger ones had thick lips and square shoulders. If a thickened lip indicates maturity, then most snails mature at about 13 mm (12 mm is the largest size at which more than half of the 1970 snails had thin lips (Figure 1-O); morphologies were not noted in 1971). The size distribution was unimodal in 1970 (Figure 1-O) and bimodal in 1971 (Figure 1-N). If the 2 modes represent year classes, then the snails grew about 10 mm during their second year. Many adults and few juveniles were found in 1970, while the same collection (from Q-8) yielded many juvenile and few adult muricids.

Nerita funiculata — Size distributions for 1970 and 1971 (Figure 1-L, M) are more similar than those for any of the other Q-8 species. Both have the same mode at 7 - 9 mm, suggesting that this species is an annual. On Barbados, 3 *Nerita* species all reach 10 - 13 mm in their first year (HUGHES, 1971b; all are mature at 14 mm or more), and similar growth rates might be expected in Costa Rica.

Fissurella virescens — These limpets (measured only in 1970) have a unimodal size distribution (Figure 1-G). No 0 - 20 mm *Fissurella* were found. Either snails did not settle during 1969 or those that did grew rapidly. *Fissurella barbadensis* Gmelin, 1791 reaches about 26 mm dur-

ing its first year and generally not more than 30 mm (HUGHES, 1971a), while *F. virescens* frequently reaches 40 mm (Figure 1-G). If *F. virescens* and *F. barbadensis* both grow at the same rate during the first year, then the 20 - 30 mm limpets from Q-11 would be yearlings.

DISCUSSION

The answer to both questions posed in the introduction is "yes." The assemblage of snails found on each quadrat in 1971 was very similar to that found on the same quadrat in 1970 — that is, much more similar than to the assemblage on any other quadrat at the same time. Furthermore, each species population was similar to the previous year's because juveniles grew and recruits settled and established themselves. The individuals I removed in 1970 were replaced by recruits prior to the 1971 collections. If these 2 quadrats are typical, then the marked faunal differences among quadrats (SPIGHT, 1977) are a persistent feature of this tropical site rather than an ephemeral feature which arises because snails are habitat generalists and are wandering from habitat to habitat.

If distributions are persistent, do they reflect habitat selection, or could they arise through less predictable processes? Habitat selection ultimately reflects factors which affect the success of a species in different habitats. Both physical and biological factors affect success, and both lead to orderly and patchy distributions in temperate communities. Each shore level has a different regime of physical stresses. Species that tolerate the dehydration and temperature stresses of one level are often unable to tolerate the greater stresses found at higher levels and may be rapidly exterminated by predators at lower shore levels (CONNELL, 1972). As a result, most species have well-prescribed vertical (shore level) ranges, and these are the basis for universal schemes of shore zonation (STEPHENSON & STEPHENSON, 1972). Similar physical regimes in the more diverse tropical community could lead to even finer vertical division of the shore habitat.

For temperate rocky shore species, physical and biotic factors also lead to patchy distributions. Recruits from many intertidal species are much more abundant in some years than others (COE, 1956; LOOSANOFF, 1964; SPIGHT, 1975), food supplies are unpredictable (SPIGHT, 1972), encounters with predators are both irregular and locally devastating (PAINE, 1974), and physical stresses are often near the tolerance limits of individuals (DAVIES, 1969; FOSTER, 1971). Within a shore level, these physical and biological stresses result in a continuing race between local extinction and recolonization (SPIGHT, 1974). Colonists

establish themselves as patches become available on the shore, and for the most part, the patches bear little relationship to the nature of the physical habitat (CONNELL, 1970; DAYTON, 1971; PAINE, 1974). With more species in the tropical community, there should be more kinds of biotic interactions, and these could, in turn, lead to more unpredictable distributions.

The changes that did take place between years (Figure 1) do imply that these same physical and biotic processes are important at Playas del Coco. Recruits from most species were much more numerous during one year than the other. *Acanthina brevidentata* was abundant on both quadrats and recruits of this species were most abundant on the 2 quadrats at different times. Thus, recruitment appears to be as unpredictable as it is in temperate waters. Tropical snails grew slowly by both measures used (tag returns and analysis of size distributions). Snails usually grow slowly because food is scarce (SPIGHT, 1972), and even a predictably sparse food supply presents a major stress. The snail sizes on Q-8 suggest recolonization after a recent burial in sand, and thus unpredictability of the physical environment. Also, more kinds of predators eat snails and together these predators are more numerous at Playas del Coco than at most temperate sites (personal observations). Activities of predators are a major cause of unpredictability in temperate waters. Appropriately, amid this array of physical and biotic stresses, the snail populations had not attained stable age distributions and showed no other evidence that the tropical rocky shore environment is more predictable for them than the temperate one.

The distributions observed at Playas del Coco were persistent, but this does not necessarily indicate that they arose by habitat selection. Patchy distributions will arise and persist despite a uniform landscape if colonizers settle patchily and subsequent species interactions maintain the patches (LEVIN, 1974). For example, unique assemblages developed and persisted in each of the artificial oak logs placed by FAGER (1968). The assemblages were best described as results of random colonization sequences to otherwise uniform habitats. Patches of some sedentary intertidal species persist for at least 6 years (PAINE, 1974). Although most species found on Q-8 and Q11 were found on both visits, the snails may have colonized these sites fortuitously; had other species arrived earlier, quite different assemblages could have developed and persisted. Therefore the present data provide no information about habitat selection and its potential role in the function of diverse tropical communities.

Persistent distributional patterns are amenable to experimental analysis, and experiments should clarify the

role of habitat selection in tropical shore communities. Transplant experiments can be united with habitat modifications and selective removals to reveal factors influencing larval settlement and adult migrations. Such experiments will add a great deal to our now meager understanding of how tropical gastropods use shore habitats.

SUMMARY

Censuses of rocky shore gastropods were taken from 2 quadrats in northwest Costa Rica in 1970 and repeated in 1971. For most species, densities and average shell lengths did not change significantly. Recruitment varied in both time and space. Growth rates of thaisids were low relative to those of temperate species, in keeping with apparent scarcity of food. Distributional patterns may reflect habitat selection by the snails, but they may also be consequences of random colonizations and subsequent biotic interactions.

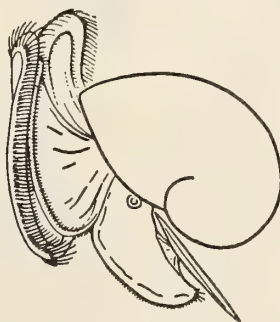
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NOTES & NEWS

A New Species Record for *Mytilopsis sallei* (Récluz) in Central America (Mollusca: Pelecypoda)

BY

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AND

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THE GENUS *Mytilopsis* is the only New World representative of the family Dreissenidae. Included in the genus are 6 New World species found from the southeast United States to Panama, and perhaps further south. All have been reported as inhabiting fresh to brackish water, all are byssiferous, and all have retained the trochophore and veliger larval stages in their invasion from the sea. All species have limited distributions, being generally confined to warm temperate or sub-tropical coastal bodies of fresh or brackish water. No overlap of species ranges has been reported, with the exception of the Panama Canal, in which both *Mytilopsis sallei* and *Mytilopsis zeteki* have been found.

Mytilopsis sallei (Récluz, 1849) was first collected by Auguste Sallé from the Rio Dulce, Republic of Guatemala. It was described as *Dreissena sallei* in 1849, and reassigned to the genus *Mytilopsis* by Conrad in 1857. Since 1849, *M. sallei* has been reported from the Gatun Locks, Panama Canal Zone (JONES & RUTZLER, 1975), and from the Visakhapatnam Harbor, India (RAJU *et al.*, 1975). In July of 1976, while studying the algal mats and stromatolites of Laguna Bacalar (18°51'N; 88°31'W), Quintana Roo, Mexico, we observed significant numbers of *M. sallei* residing on the soft benthic sediments of the lake. Specimens were collected and preserved for later examination. Identification was made with the help of species descriptions and comparison with specimens

of *M. leucophaetus*, with which *M. sallei* is often confused.

This location (Laguna Bacalar) represents a new record for *Mytilopsis sallei*. Its distribution in and around the lake has not been examined, but zoological work on this bivalve is forthcoming.

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Protoconch of Ovoviviparous Volutes of West Africa

BY

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(1 Text figure)

THERE HAS BEEN a tendency among malacologists to interchange the words protoconch and nucleus. One glossary (BURCH, 1950) describes nucleus as "Apex or first part of the shell formed by the embryonic animal;" another (ARNOLD, 1966) as "the tip or earliest formed part of a shell." In most species this is true. Therefore, it was interesting to note that in ovoviviparous volutes of the genus *Cymbium* observed in West Africa, the protoconch was the last part formed.

From the bodies of females, young were removed in various stages of development from yolk to completely formed animals with shells. In several instances the shells were found completely formed except for the protoconch. A ball of yolk rested where the protoconch would be formed ultimately. A thin wall of shell was formed between the ball of yolk and the remainder of the shell. A number of these was taken from different females. At least 2, developed to this stage, were brought back by the expedition.

In the newborn *Cymbium*, the protoconch is the most fragile part of the shell, being paper thin. If crushed, a ball of yolk is disclosed underneath.

ACKNOWLEDGMENTS

I wish to express my appreciation to Yvonne Albi for the accompanying sketches.

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Figure 1

A & B - Newborn *Cymbium pepo* [Lightfoot, 1786], with fragile protoconch
C through G - Unborn *Cymbium marmoratum* (Link, 1807) with shell developed except for protoconch

size $\times 0.8$

A. S. Z.

RICHMOND MEETING
of the American Society of Zoologists,
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and the American Microscopical Society

THE AMERICAN SOCIETY of Zoologists, Society of Systematic Zoology, and the American Microscopical Society will meet at the Hotel John Marshall in Richmond,

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and the Analysis of Adaptation; Microscopical Structure and Distribution of Silicon in Biological Systems; and the Contribution of Electron Microscopy to Systematics. In addition, a Workshop on Major Problems in Crustacean Biology is being planned.

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Subscription rate to Volume 21 is \$30.- plus postage.

We must emphasize that under no condition can we accept subscription orders or membership applications for calendar year periods. If "split volumes" are required, we must charge the individual number costs. Individual issues sell at prices ranging from US\$12.- to US\$24.-, depending on the cost to us.

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of the remittance. The same policy applies to new members.

THE VELIGER is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of \$1.- to a percentage of the value of the draft, going as high as 33%. Therefore we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of United California Bank in Berkeley, California. This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable except as indicated elsewhere in this section.

Publication Date of THE VELIGER

THE PUBLICATION DATE of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is

available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US\$8.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US\$18.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

Claims for defective or missing pages must reach us within 60 days from the publication date. We will not respond to claims of missing issues made less than 30 days by domestic addressees, or less than 60 days by foreign addressees after the publication date of our journal issues. This refusal is necessary as we have received an increasing number of "claims" as much as 6 months before the claimed issue was to be published. We wish to conserve our energy and the cost of postage and stationery for more productive purposes.

Supplements

Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

Requests to be placed on this special mailing list should be sent to Dr. George V. Shkurkin, *Manager*, 1332 Spruce Street, California 94709

However, until further notice, we are suspending the publication of supplements until it will be reasonably certain that we will not be forced to spend many hours in tracing of lost insured or registered parcels and entering claims for indemnification. The special mailing list of members

and subscribers who have entered an "including all supplements" will be preserved because of our innate optimism that sometime within our lifetime the postal services throughout the world will return to the former excellent and reliable performance.

Moving?

If your address is changed it will be important to notify us of the new address at least six weeks before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. Effective January 8, 1968 the following charges must be made:

change of address - \$1.-

change of address and re-mailing of a returned issue - \$2.75 minimum, but not more than actual cost to us. We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

At present we are charged a minimum fee of \$12.50 on each order for new addressograph plates. For this reason we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

The regulations pertaining to second class mailing require "pre-sorting" of the mail which involves a large amount of time, especially if the total number of pieces is too small to warrant the employment of computerization. This requirement seems justified as long as the rates for second class matter remain substantially below those for first class matter. However, our members should be aware of the fact that postal regulations rule that second class matter can not be forwarded three months after an address change, even though the addressee guarantees forwarding postage (in contrast, first class mail, at least for the time being, is forwarded for one year and that without charge!). Thus, issues mailed to the "old" address will be returned to the publisher if return postage is guaranteed at a rate that is considerably higher; we have been charged as much as \$1.45 for such returned copies. There is also a charge of 25¢ for a postal notification of the new address. It must be obvious that we cannot keep absorbing such extra expenses and keep membership dues and subscription rate at the current low rate. We must ask for the wholehearted cooperation of all concerned to help us to hold the line against increases. Also, if a copy is returned we will, as in the past, advise the member of this fact and indicate the total costs incurred for which we must seek reimbursement. If this reimbursement is not made, we cannot continue to send future issues to the delinquent member. Membership will have to be considered as terminated and can be re-instated only upon payment of all arrears. We regret that this apparently hard rule is necessary, but we wish to continue publishing the Veliger - which will not be possible if these rules are not observed.

CALIFORNIA

MALACOOZOLOGICAL SOCIETY, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, the VELIGER. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C. M. S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, devices are deductible for Federal estate and gift tax purposes under section 2055, 2106, and 2522 of the Code. The Treasurer of the C. M. S., Inc. will issue suitable receipts which may be used by Donors to substantiate their respective tax deductions.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15 but before March 15 of the following year, there will be a re-instatement fee of \$1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of \$5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is \$25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of \$4.25 (to reimburse us for the expenses involved in redeeming them) and at \$0.95 per \$1.- face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time, that is 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed \$200., the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, \$200.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U. S. A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are sub-

mitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript — including figure explanations and the "Literature Cited" section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the "dead letter" office, in other words, it is destroyed.

BOOKS, PERIODICALS, PAMPHLETS

Endodontoid Land Snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra)

Part I

Family Endodontidae

by ALAN SOLEM. Field Museum of Natural History, Chicago, Illinois. pp. xii + 1 - 508; 208 text figures; 114 tables; 23 × 32.5 cm. \$31.50, postpaid (29 Oct. 1976)

As indicated in the extended title of this publication, a second part is in preparation. That part will deal with the families Punctidae and Charopidae. Part I, the present work, deals exclusively with the Endodontidae. The study is based on over 26000 specimens and both parts together will report on 45 genera including 285 species. The terms "genus" and "species" include "subgenus" and "subspecies." Of these taxa, 84% of the genera were not previously recorded, and 54% of the species are new to science. In the present volume 19 genus level and 102 species level taxa are recognized as new.

While these statistics might be interpreted that the author is an extreme splitter and that the work harks back to 19th century taxonomy — nothing could be fur-

ther from the truth. This becomes evident in the first three chapters, entitled: Previous Studies; Material Studied; and Methods of Analysis. Decisions are not based on subjective impressions supported by cursory examinations with a hand lens. Nor are taxa established on the basis of a single chance specimen.

For a critical evaluation of the validity of the work it is important to carefully study the 80 page chapter entitled Patterns of Morphological Variation. It is made clear in these pages how many different characteristics have to be taken into account and the rather staggering amount of careful observations combined with highly critical analyses that have gone into each decision. Support is adduced with the aid of the most modern technical means available – statistical analysis, scanning electron microscopy, as well as, of course, the traditional methods.

A brief chapter on Habitat Range and Extinction shows how little may be required to wipe out a species, but it also leaves the clear impression that in the majority of cases it is human influence that is the causative agent. Deforestation coupled with advancing agriculture eliminates the normal ecological conditions required by these highly specialized small animals. There is left little doubt in the mind of this reviewer that some of the taxa described as new in this monumental work have already been wiped out (many of the specimens used in this study had been collected in the first half of the current century). It also becomes clear why there seems to be a sudden increase in the number of taxa – most of these small snails occur in areas that have been difficult to reach and to explore; further, collecting them requires painstaking work with heavy investment of time in the field.

The chapter on Phylogeny and Classification takes up 19 pages. Here computerization is used for the production of a possible "family tree."

The largest chapter is, of course, the Systematic Review, which takes the next 367 pages. Even a casual scanning reveals the thoroughness and critical care of the work. The superb drawings are convincing even the most skeptical student. Well executed graphs help make clear the points the author is making. While the treatment of each species-level taxon is divided into the usual parts – diagnosis, description, holotype, range, paratypes, material, and remarks – the thoroughness and clarity of each treatment are outstanding.

The remainder of the work is divided into a brief chapter on Zoogeography (5 pages), a list of References (7 pages), a Systematic Index (about 6 pages), a Geographic Index (a trifle more than one page), with a

half-page Summary and a page of explanations of the anatomical terms used in the illustrations.

It is our opinion that Dr. Solem's work will be considered a classic in its field and that it will be accepted as a standard of the best of twentieth century taxonomy. He is to be commended on his industry and endurance, which were needed to bring this work to its successful completion.

R. Stohler

Marine Shells of Southern California

by JAMES H. McLEAN. Natural History Museum of Los Angeles County, Science Series 24, Revised Edition: 1 to 104, 54 figures in text. \$5.00. (20 March 1978)

A compact and well-organized guide to some 318 species of mollusks of the southern California area, this work has brief descriptions and figures, with notes on habitat and range of all of the commoner intertidal forms in that region. Some that are less common and some from offshore also are included. The half-tone figures, from photographs, are grouped in the text-figures either on the same page as, or adjacent to the descriptions; all are clear enough for ready identification of species, even for the smaller forms.

Although this is in the main a reprint of the 1969 first edition, nomenclature is updated. Changes of names that had become necessary are detailed in a new preface; also, notes on recent collecting regulations are given. The demand that soon exhausted the first edition showed how much a good local guide had been needed, and the author is to be commended for his skillful planning of a work useful to both the novice and the more experienced collector.

A. Myra Keen

The Turridae of the European Seas

by FRITZ NORDSIECK. La Conchiglia, Rome. 131 pages; 144 pen-and-ink drawings on 26 plates. No price given. 1977 (probably late November)

According to the postal marking, the book was mailed in Rome, Italy on November 30, 1977. It reached our desk on March 24, 1978, having been underway for almost a full 4 months. Unfortunately, the book, which measures

14 × 21 cm, was obviously soaked in water somewhere in transit. The text and figures are printed on coated stock, as a consequence of which the pages are stuck together and it is impossible to separate the pages from each other without severe damage to legibility of text and precision of figures. If we, nevertheless, try to give what we consider a fair appraisal, it must be understood that this is based more on the earlier similar work by the same author, the 4 volumes we reviewed in our volumes 11, 12 and 16. As far as it is possible to ascertain, the format of the present work is identical with that of the ones to which we just alluded. The main difference seems to be that this work is limited to one family, which, from the foreword, is to complete the work begun in the earlier volumes. It is intended as a "chapter" of the total work and includes 10 subfamilies, 59 genera and subgenera, 305 species and subspecies.

It is probably safe to assume that, as before, there are many new taxa proposed in this book. On 2 pages which we were able to separate from each other more or less successfully, we find 10 subfamilies, 36 genera and 24 subgenera. Of these, 2 are new names and 4 are new subgenera. It is possible to "peek" between portions of pages in a few places. In every case it is possible to discern the symbol *n. sp.* after some names. But, unfortunately, the author also continues to establish "Forms" which have no standing in taxonomy. It may be assumed that this is done for the "benefit" of amateur shell collectors.

In spite of this latter drawback, we think that the book will fill a useful purpose.

R. Stohler

Malacological Review

Vol. 10 (1-2): 224 pages; numerous figures in text. 1977.

Published at the Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109, U. S. A., by the Society for Experimental and Descriptive Malacology.

Orders and subscription should be addressed to Dr. J. B. Burch, P. O. Box 420, Whitmore Lake, Michigan 48189, U. S. A.

The first article reviews the literature pertaining to the European pulmonate snail *Helix pomatia*. There are brief but cogent annotations to each citation. Six research articles follow: 2 deal with ecological factors inducing aestivation in *Ferrisia wautieri*; one deals with tolerance of *Biomphalaria glabrata* embryos of thermal stress; another describes 13 new species of land snails from the southeastern United States; the fifth article reports on intramarsupial suppression of fetal development in sphaeriid clams, while the concluding paper deals with anatomical systematics of *Cristaria plicata*.

There follow brief communications, 4 in number and the section News and announcements, Miscellanea, Obituaries and Book Reviews make up the remainder of the first section. The second section, as usual, is given over to a reproduction of the tables of content of 27 periodical publications in malacology on a worldwide basis. A very useful feature is the list of authors of all publications listed in the reproduced indices, giving the addresses of the authors. This should help prevent useless correspondence to editors requesting reprints, which should in most, if not in all, cases be sent to the respective authors. Some 11 pages list publications other than those found on the index pages. The concluding 3 pages are devoted to an index of the scientific names used in the research article.

We were especially pleased to see on the inside back cover a requirement that we have long considered: voucher specimens of all species used in all papers must be deposited in a recognized repository. At the Veliger we have made this a recommendation, so far, as we have been unable to ascertain how many such repositories are available and what degree of checking the material for glaring errors in identification might be provided. But we certainly applaud this requirement and consider it long due.

R. Stohler

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in **THE VELIGER** is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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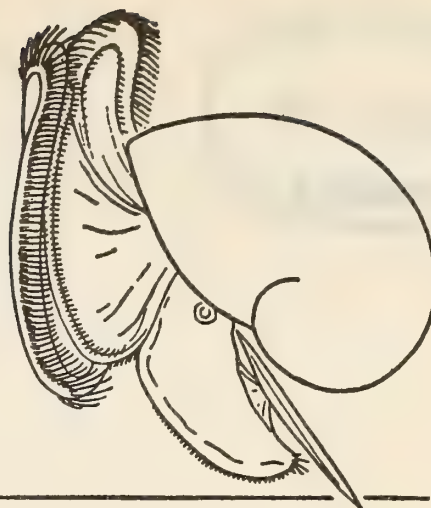
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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, Genus, (Subgenus)
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Papers on Neogene Mollusks of the North Pacific Margin: An Introduction

BY

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THE EIGHT PAPERS dealing with Neogene (Miocene and Pliocene) molluscan paleontology and biostratigraphy of the North Pacific margin included in this issue were presented at the First International Congress on Pacific Neogene Stratigraphy held in Tokyo, Japan, May 17-21, 1976. These papers interrelate the Neogene biochronologies of different sectors of the North Pacific and trace the origin and development of the highly endemic Neogene molluscan faunas of this region. Moreover, they provide an overview of the status of knowledge of Miocene and Pliocene mollusks of the North Pacific and bring into focus the importance of molluscan research as a key to improved understanding of the Neogene history of the Pacific basin.

Two papers synthesize data on the faunal sequences of the northern margin of the Pacific (Alaska) and the middle latitudes of the western north Pacific (Japan). Kiyotaka Chinzei's paper on the Japanese Neogene brings together the extensive biostratigraphic data from the Japanese Islands to detail the geographic shifts of warm and cool water faunas in response to climatic change. He also distinguishes ocean, coastal, and embayment molluscan faunas in addition to benthic communities related to bottom topography and sediment texture. Richard Allison's review and analysis of molluscan data from coastal Alaska clarifies the age and correlation of Neogene formations and sets the stage for much-needed detailed paleontologic study of the rich, mollusk-bearing sequences of the Gulf of Alaska and the Alaskan Peninsula.

Papers by Tamio Kotaka, Koichiro Masuda, and Clifford Nelson deal with three of the best groups of mollusks for provincial and interregional correlation: the Turritellidae; Pectinidae, and Neptuneidae, respectively. The neptuneids seem to be best suited for interrelating the faunal sequences of the cool, high latitude parts of the North Pacific and show promise of striking comparisons with the North Atlantic. Turritellids, by virtue of their warmer water distributions are most useful in the biochronology of the middle and low latitudes, as indicated by Kotaka.

The Pectinidae are excellent biochronologic indicators in all latitudes although Masuda shows that their Neogene distribution in the higher latitudes of the North Pacific is most promising in circum-North Pacific correlation.

Temporal calibration of the molluscan sequence of southern Japan with the standard European Neogene sections through tie-ins with planktonic foraminifers is treated by Ryuchi Tsuchi and Masako Ibaraki. This paper exemplifies the kind of research that is needed to correlate the oceanic microfossil sequences defined by recent deep-sea drilling, with the shallow water, nearshore sequences that are best characterized by mollusks and other larger invertebrates. Some aspects of high latitude correlation by mollusks and siliceous microfossils such as diatoms are considered by Yuri Gladenkov based on studies of the Neogene of Kamchatka and Sakhalin.

The origins of the diverse and well-known Pliocene molluscan fauna of northern Japan are found in genera that evolved in the western North Pacific during the late Paleogene and early Neogene or which migrated into this region from the Tethyan region to the southwest. According to Frank Kilmer the chronology of dispersal events of these Tethyan genera is similar to that observed in New Zealand but the rates of generic extinction are dissimilar. These papers were presented at sectional meetings on mollusks at the Neogene Congress which were attended by 30 to 40 specialists, mostly from the western North Pacific. As a consequence of the intense interest in Neogene molluscan phylogeny, biostratigraphy, and biogeography generated by these presentations, a cooperative effort to make these data and interpretations more widely available through publication was undertaken by Tsugio Shuto and myself. The only previously available information was in the form of brief resumes (see SARTO & UJNÉ, 1977). These sessions also led to extended discussions of molluscan distributions around the North Pacific rim and to the formation of two working groups to stimulate and coordinate this kind of research: a working group on Mollusca (co-chairmen Sa-

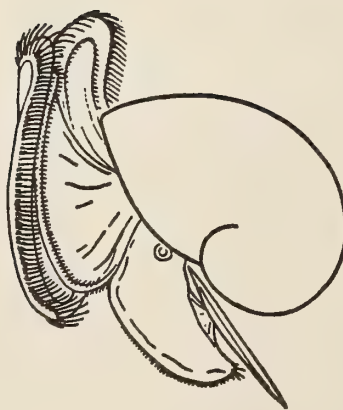
buro Kanno and W. O. Addicott) and a working group on North Pacific correlations of on-land Neogene sequences (co-chairmen R. C. Allison and Yuri Gladenkov).

I am indebted to my co-editor, Tsugio Shuto of Kyushu University, Japan, for his helpful cooperation in planning the publication of these papers on Neogene mollusks. His report on the marine Neogene of southeast Asia, presented to the general session at the Tokyo meetings (SHUTO, 1977), complements the western North Pacific summaries of Chinzei, Tsuchi and Ibaraki, and Gladenkov that appear in this issue. Similarly, a summary of the Neogene molluscan chronologies of the Pacific Coast States (ADDICOTT, 1977) complements Allison's synthesis of Alaskan molluscan biostratigraphy. Thanks are also due to the Regional Committee on Pacific Neogene Stratigraphy, and to its

Chairman Nobuo Ikebe and Secretary-General Yokichi Takayanagi for their encouragement and support without which publication of these papers would not have been possible.

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Neogene Molluscan Faunas in the Japanese Islands: An Ecologic and Zoogeographic Synthesis

BY

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(8 Text figures)

INTRODUCTION

A VAST AMOUNT OF INFORMATION on the Japanese Neogene molluscan faunas has been accumulated since the late Professor Matajiro YOKOYAMA first described the Neogene mollusks from the Miura Peninsula, south of Tokyo, in 1920. In 1939, OTUKA outlined the Cenozoic marine and terrestrial faunas in Japan. He recognized two or three marine faunal provinces and showed different faunal sequences for each province. His synthesis had a marked influence on later work. Since then, many investigators have tried to synthesize the historic and geographic distributions of the Neogene mollusks in Japan. Some of these syntheses are, however, biostratigraphically oriented with little attention to the environmental background of the faunas (e.g., IKEBE, 1954; ASANO & HATAI, 1967), and others are geographically, stratigraphically, or taxonomically limited (e.g., KOTAKA, 1958, 1959; MASUDA, 1962; UOZUMI, 1962; CHINZEI, 1963; NODA, 1966; ITOIGAWA & SHIBATA, 1973). MASUDA (1973) discussed the geographic and stratigraphic distributions of the principal molluscan species in Japan, and divided the Japanese Neogene into 5 stratigraphic units.

In this paper I intend to present a general picture of historic and geographic changes of the Japanese Neogene molluscan faunas in view of ecologic characters of the faunal constituents, and their local and regional distributions.

The Neogene deposits of the Japanese Islands exhibit a major cycle of sedimentation. The cycle began in the early middle Miocene with rapid subsidence followed by gradual filling of the sedimentary basins. This general tendency was modified by local up- and down-movements in both basins and area of provenance. The geographic and stratigraphic distributions of the benthic molluscan faunas were primarily controlled by the history of sedimentation, and the characteristics of the water masses surrounding the

Japanese Islands. Ecologically analogous associations, or fossil communities, occur at distinct stratigraphic levels where similar environmental conditions repeatedly appeared.

The analogous associations consist of different species belonging to the same genus or to allied genera whose ecologic requirements were essentially the same. They are found in the same sedimentary facies, such as offshore muddy facies, fine-grained sand facies of shallow embayments etc., at different horizons in the different areas. Thus the analogous relationships of these associations may be compared with ecologically parallel relationship observed among the Recent marine communities (THORSON, 1957).

Based on this repetition, the Neogene molluscan faunas of Japan can be grouped into 4 faunas of different ages. These faunas represent 4 phases in the historical change of our Neogene Mollusca. They are the early Miocene fauna (occurring somewhere between 26 and 16 my), the early middle Miocene fauna (c. 16-14 my), the late Miocene fauna (12-5 my), and the Pliocene to early Pleistocene fauna (5-1 my). The late Pleistocene and Recent faunas may be regarded as a 5th fauna and represent the latest stage of our faunal history.

On the other hand, the faunas of two different water systems, warm and cold, are recognized throughout the Neogene as well as today. The ecologically analogous relationships are also observed between the warm and cold water fossil faunas. By tracing changes in faunal characters we can follow the sequential shift of water masses around the Japanese Islands.

The chronology of the molluscan faunas and fossiliferous strata is based on the correlation table compiled by IKEBE *et al.* (1972), and revised according to later information. The correlation was made principally on the basis of planktic foraminiferal biostratigraphy supplemented by the data from other microbiostratigraphy and radiometric dating. Since the molluscan fossils are frequently found in

the shallow water facies, their chronologic positions are not always determinable by planktic foraminifers. In such cases, the fossiliferous beds were placed chronologically based on local stratigraphic relationships and other indirect evidence.

EARLY MIOCENE FAUNAS

The early Miocene deposits are of limited distribution in the Japanese Islands, and their chronostratigraphy has not been established. The molluscan faunas also have not been very well documented. The faunas are associated with a minor transgression which was antecedent to and independent from the major middle to late Miocene transgression.

In northern Kyushu, a marine formation, the Ashiya Group, overlies thick coal-bearing formations of Paleogene age. The Group contains a shallow water molluscan fauna, the Ashiya fauna. The geologic age of the Group has been regarded by some as late Oligocene, by others as early Miocene. Recent studies have revealed that in the Nichinan area of southern Kyushu (Loc. 3, Figure 1), mollusks in common with the Ashiya Fauna are associated with the early Miocene planktic foraminifers, *Globigerinita dissimilis*, *Globigerina hohri*, and a few others (SHUTO, 1963).

Medium-grained sandstone at the type locality of the Group (Loc. 1), is rich in mollusks, *Glycymeris cisshuensis*, *Solen connectens*, *Dosinia chikuzenensis*, *Pitar matsumotoi*, *Lucinoma nagaoi* and other suspension feeding bi-

valves (SHUTO & SHIRAISHI, 1971). The association may represent the sandy bottom community of a shallow sea. Black sandy mudstone of the Ashiya Group in the Kottoi area (Loc. 2) contains *Venericardia subnipponica* and *Angulus maximus* with *Cultellus izumoensis*, *Acila ashiyaensis*, and *Sacella* sp. (OKAMOTO, 1970). They are associated with lenses of *Crassostrea* sp. *Batillaria takeharai* is found in sandstone around the oyster banks. The *Venericardia-Angulus* association may be a member of a subtidal muddy bottom community of an embayment. *Crassostrea* and *Batillaria* may represent an associated intertidal community.

A molluscan fauna, which has been regarded as early Miocene, is known from the Chichibu Basin (Loc. 5; KANNO, 1960) and the Moriya area (Loc. 4), both in central Honshu. They are different in species composition from the Ashiya Group except for some common species, such as *Pitar matsumotoi*, *Dosinia chikuzenensis*. The fauna is characterized by *Anadara chichibuensis*, *Acila submirabilis*, *Venericardia tokunagai*, *Dosinia chikuzenensis*, and other coastal water sandy bottom bivalves. The stratigraphic relationship between the Chichibu-Moriya and the Ashiya Faunas is uncertain.

The Ashiya Fauna and the Chichibu-Moriya Fauna were most probably associated with warm water judging by the lack of apparently northern species and by the common or dominant occurrence of such warm water genera as *Anadara*, *Pitar*, and *Dosinia*.

Little is known about the offshore associations of early Miocene age. *Portlandia tokunagai*, *P. watasei* and some other nuculanid bivalves with *Periploma besshoensis* and *Macoma optiva* have been reported from several places along the Pacific coast including the Chichibu Basin in the mudstone referred to the lower Miocene. No reliable data, however, have been available on their bathymetric ranges and on the habitat relationship between the sandy shallow water faunas. Since *Portlandia tokunagai* and *P. watasei* are known from Sakhalin and Kamchatka (GLADENKOV, 1974), these species probably lived in the cold water areas. The northern species tend to live at progressively greater depths toward the south, a relationship that exists in the present-day marine environment. In the Recent environment, a submerged tongue of cold water, the Oyashio Undercurrent, has been recognized under the surface Kuroshio Current at about 300 to 1000 m off the east coast of central Honshu. The tongue brings benthic and planktic subarctic species southward as exemplified by OKUTANI (1972). It is natural to infer that *P. tokunagai* and its associated species extended their distribution southward into deep water by means of the cold water undercurrent.



Figure 1

Distribution of the early Miocene molluscan faunas and presumed paleogeography of Japan during the early Miocene. Numerals indicate the fossil localities mentioned in the text; 1: Ashiya; 2: Kottoi; 3: Nichinan; 4: Moriya-yama; 5: Chichibu; 6: Asahi; 7: Chikubetsu

Occurrence of a shallow cold water molluscan fauna, named the Asahi Fauna, is known in central Hokkaido (Loc. 6). The fauna has been assigned to the early Miocene. No positive evidence, however, has been given on the geologic age of the fauna. It is contained in the Asahi Formation, the basal part of the Neogene marine sequence in central Hokkaido (UOZUMI, 1966; KANNO *et al.*, 1968). The formation yields *Mytilus tichanovitchi* associated with *Peronidia t-matsumotoi*, *P. elongata*, *Spisula onnechiuria*, *Thracia asahiensis*, *Tectonatica ezoana*, and other less abundant species. A similar association was reported from the Sankebetsu Formation in the Chikubetsu area of north-western Hokkaido (Loc. 7), although *M. tichanovitchi* was not found there (KANNO & MATSUNO, 1960). The generic composition as well as the characters of the contained sediments indicate that the association represents a coastal water fauna.

The Asahi Fauna is quite different in species composition from the Ashiya Fauna as well as from the overlying early middle Miocene subtropical fauna which will be mentioned later. The species of the Asahi Fauna are limited in their distribution to Hokkaido or farther north. *Mytilus tichanovitchi* is reported from northern Sakhalin and Kamchatka (e.g., MAKIYAMA, 1934; GLADENKOV, 1974). The association is thus considered to represent a cold water fauna. The offshore type *Portlandia tokunagai* association is also found in the muddy facies of the Asahi and the Sankebetsu Formations.

EARLY MIDDLE MIOCENE FAUNAS

The early middle Miocene was a turning-point in the Japanese Neogene history. It was the start of geosynclinal sinking in Northeast Japan and along the Japan Sea coast, and the start of transgression onto the denuded hilly lands in the central part and on the Pacific coast of Southwest Japan. Shallow marine sediments cover the subaerial volcanic and clastic deposits, or the pre-Tertiary rocks.

The transgressive marine deposits contain abundant molluscan and other benthic faunas of shallow water type. The faunas are dominated by tropical and subtropical elements and they spread over most of the Islands (Figure 2). No true reef facies have been found in the main Japanese islands. The cold water fauna occurs only in northern Hokkaido, and the offshore associations in northern and central Honshu and Hokkaido.

Tropical molluscan associations were described by TSUDA (1960) from the Yatsuo area (Loc. 13), on the Japan Sea coast of central Honshu. In the Yatsuo area poorly sorted, dark grey muddy sandstone interdigitates with

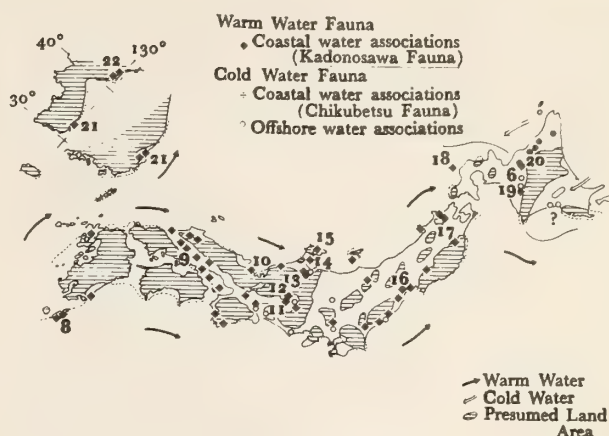


Figure 2

Distribution of the early middle Miocene molluscan faunas and presumed paleogeography of Japan during the early middle Miocene. Numerals indicate the fossil localities mentioned in the text; 8: Tanega-shima; 9: Shobara; 10: Ogurui; 11: Morozaki; 12: Mizunami; 13: Yatsuo; 14: Nanao; 15: northern tip of the Noto Peninsula; 16: Moniwa near Sendai; 17: Kadonosawa; 18: Okushiri Island; 19: Takinoue; 20: Uryu; 21: Gampo; 22: Myonchon

the conglomerate of deltaic facies. The sandstone contains *Geloina stacki*, *G. yamanei*, *Anadara daitokudoensis*, *Telescopium schenki*, *Vicarya yokoyamai*, *Cerithidea yatsuoensis* and other gastropods and a few bivalves. The association is comparable with the present-day mangrove swamp community (OYAMA, 1950), and indicative of the tropical nature of the early middle Miocene faunas. The same *Geloina* association was reported from the Shobara area in western Honshu (Loc. 9).

Other tropical mollusks were reported from the Ogurui area (Loc. 10; KOBAYASHI & HORIKOSHI, 1958). They are *Globularia nakamurai*, *Conus cf. jenkinsi*, *Rochia japonica*, *Turbo cf. ticaonica*, and the nautiloid *Aturia minoensis*. The gastropods are all equatorial genera that live on clean sandy bottoms facing an open sea. *Globularia nakamurai* was also found in the Shobara area (Loc. 9).

The characteristic elements of the mangrove swamp community, *Geloina* and *Telescopium*, are restricted to central and western Honshu, while the other species, such as *Anadara* and *Vicarya*, are known over the Japanese Islands as far north as southern Hokkaido. In Okushiri Island, Hokkaido (Loc. 18), *Anadara daitokudoensis*, *Soletellina minoensis*, *Vicaryella notoensis*, *Vicarya yokoya-*

mai, and some other species are found in dark grey, fine-grained sandstone, associated with oyster banks (UOZUMI & FUJIE, 1966). The composition of the association is typical of the *Anadara-Vicarya* association found in other areas of Japan, and is an example of a subtropical tidal flat community.

The habitats of subtropical coastal water communities and their areal distribution were reconstructed in the Kadonosawa Basin of northern Honshu (Loc. 17). In this basin, the basal bed of the marine Kadonosawa Formation was deposited in a small U-shaped embayment (Figure 3). Five autochthonous molluscan associations have been distinguished in this basal bed (CHINZEI & IWASAKI, 1967).

The black muddy sandstone distributed in the bayhead and the marginal parts contains *Batillaria yamanarii* and *Macoma* cf. *incongrua* associated with *Soletellina minoensis*, *Saxolucina k-hataii*, *Cyclina japonica*, *Ringicula ninohensis*, and *Vicarya callosa japonica*. The association is dominated by deposit feeding species. Although *Ana-*

dara daitokudoensis has not been found, the association is equivalent to the *Anadara-Vicarya* association, and represents the tidal flat community. In front of the tidal flat facies, there are banks of a thick-shelled oyster, *Crassostrea gravitesta*. Oysters are found as clusters in grey muddy sandstone. *Compsomyx iizukai*, *Panopea kanomatazawaensis*, and *Euspira meisensis* are found among the oysters.

The main part of the restored bay is occupied by non-stratified, grey muddy fine-grained sandstone. The sandstone contains abundant shallow-burrowing suspension feeding bivalves including *Dosinia nomurai*, *Clinocardium shinjiense*, *Anadara ninohensis*, *Compsomyx iizukai*, and *Tapes siratoriensis*. Other species, such as, *Panopea kanomatazawaensis*, *Glycymeris cisshuensis*, and *Euspira meisensis*, are also commonly found. Solitary shells of *Crassostrea gravitesta* occur sporadically in the fossiliferous sandstone. This association is considered a sandy bottom community that lived in the central part of the shallow bay. Clusters of *Felaniella usta* occur in well sorted medium-grained sandstone near the bay-mouth. *Felaniella* is associated with *Conus tokunagai*, *Tapes siratoriensis*, and *Euspira meisensis*.

In sandy mudstone outside of the bay, there is an association composed of *Macoma optiva* with *Lucinoma annulata*, *Mizuhopecten kimurai*, and *Anadara* sp. This association represents a shallow muddy community in the Kadonosawa Basin.

The fauna has been called the Kadonosawa Fauna (OTUKA, 1934), and is considered representative of the Japanese early middle Miocene subtropical faunas. The Kadonosawa type molluscan fauna is known from more than 30 localities in Japan as shown in Figure 2. The fauna in one locality is usually composed of two or three associations corresponding to associations in the Kadonosawa Basin. Mixed occurrences of the species which constitute the different associations in the Kadonosawa Basin are also commonly found. The mixing might have happened in some cases during sedimentation.

The northernmost distribution of elements of the subtropical Kadonosawa Fauna is in the Uryu Coal-Field, central Hokkaido (Loc. 20; OHARA & KANNO, 1973). In this area, sandstone of the lower middle Miocene Shinuryu Formation contains *Anadara ogawai*, *Dosinia nomurai*, *Tapes siratoriensis*, and *Euspira meisensis*; this association is analogous to the *Anadara-Dosinia* association in the Kadonosawa area. A similar molluscan fauna is known from the Takinoue Formation (Loc. 19) which overlies the Asahi Formation containing the cold water Asahi Fauna. In the Takinoue Formation elements of the *Batillaria* association, *Batillaria yamanarii* and *Macoma incongrua*, etc., have been reported in addition to *Dosinia nomurai*, *Tapes siratoriensis* and other sandy bottom mollusks

MOLLUSCAN ASSOCIATIONS

- △ *Batillaria*
- *Crassostrea*
- ⊕ *Anadara - Dosinia*
- *Felaniella*
- *Macoma - Lucinoma*

LITHOFACIES

- ▨ Sandy mud
- ▤ Black muddy sand
- ▥ Grey muddy sand
- ░ Clean sand
- ▧ Gravelly sand



Figure 3

Distribution of the coastal water associations in the basal part of the early middle Miocene Kadonosawa Formation in the Kadonosawa Basin (Locality 17), north of Honshu. Thick line indicates the presumed coastline. Redrawn from CHINZEI & IWASAKI (1967)

(KANNO & OGAWA, 1961). Mollusks from Tanega-shima (Loc. 8), south of Kyushu, are the southernmost record of the Kadonosawa Fauna (HAYASAKA, 1969). Included are *Anadara daitokudoensis* associated with *Vicarya callosa japonica*, *Cerithidea shirakii*, and some other potamid gastropods with banks of *Crassostrea gravitesta*.

The Kadonosawa Fauna is known along the Japan Sea coast of the Korean Peninsula. In the Gampo area, south-eastern Korea (Loc. 21), the middle Miocene Eoil Formation contains the *Anadara-Vicarya* association identical to the Japanese tidal flat community, as well as beds of *Crassostrea gravitesta* (KIM *et al.*, 1974). The same association was reported from the basal part of the Miocene Meisen Series in the Myonchon (Meisen) area of northern Korea (Loc. 22). Many of the characteristic species of the Kadonosawa Fauna were first described from here by MAKIYAMA (1926, 1936). The upper part of the Series is rich in late Miocene cold water mollusks as discussed later.

A belt of marine sedimentation was formed through western Honshu in an east-west direction during the middle Miocene. This belt of sedimentation is called the Setouchi Province, antecedent of the present-day Setouchi Inland Sea. The marine deposits of the Setouchi Province contain abundant molluscan fossils, especially in the lower part, the transgressive lower middle Miocene. ITOGAWA & SHIBATA (1973) distinguished 16 associations in the Mizunami and surrounding area, eastern Setouchi Province (Loc. 12), ranging in habitat from intertidal to uppermost bathyal and from gravel-rock to muddy facies. Thirteen of these are shallow water associations. They are basically comparable with those in the Kadonosawa area, but there are some differences in species composition. Among the associations they described, that dominated by *Saccella miensis*, *Venericardia siogamensis* and *Cultellus izumensis*, associated with *Macoma optiva* and *Lucinoma acutilineatum*, is typical of the shallow water muddy bottom community. The subtidal muddy bottom association is poorly represented in the Kadonosawa and other areas. In detail, the muddy bottom association is divided into two parts, the *Saccella-Cultellus* and the *Macoma-Lucinoma* associations (ITOIGAWA, 1974). The latter probably lived in deeper water than the *Saccella-Cultellus* association.

Gravel bottom communities are characterized by the abundant occurrence of pectinid species. In the Nanao area (Loc. 14) of the Noto Peninsula, central Honshu, *Nanaochlamys notoensis*, *Kotorapecten kagamianus*, *Placopecten akihoensis* occur in loose, pumiceous sandstone (MASUDA, 1962). The association is typical of the subtropical shallow sea pectinid-rich communities; associations of similar composition have been recorded from many places in northeastern Honshu and southern Hokkaido (MASUDA,

1962). Conglomeratic sandstone of the Moniwa Formation near Sendai (Loc. 16) is an example. It yields *Chlamys arakawai*, *C. cosibensis*, *Aequipecten yanagawaensis*, in addition to the species known from Nanao. Rocky bottom communities are uncommon among the early middle Miocene faunas. MASUDA (1966) described the rocky bottom mollusks from the tip of the Noto Peninsula (Loc. 15), where *Haliotis notoensis*, *Turbo ozawai*, *Nerita ishidae*, and *Cypraea ohiroi* are found in association with fragments of corals, larger foraminifers in the conglomeratic sandstone of the Higashi-Innai Formation.

The cold shallow water molluscan fauna of early middle Miocene is known only in northern Hokkaido. In the Chikubetsu area (Loc. 7), the middle Miocene Chikubetsu Sandstone contains *Spisula onnechiuria*, *Peronidia tsumotoi*, *Mercenaria chitaniana*, *Mya cuneiformis*, *Tectonatica ezoana*, *Neptunea oomurai* and some other mollusks (KANNO & MATSUNO, 1960). The mollusks are shallow water inhabitants judging by the generic composition and lithologic characters of the enclosing sediments. However, there are no species in common with the Kadonosawa type sandy associations, and the Chikubetsu Fauna is thus considered to be the cold water counterpart of the subtropical sandy bottom communities. The same cold water association was reported from the lower part of the Shinuryu Formation in the Uryu area (Loc. 20). It is worthy of note that in the Shinuryu Formation, the Kadonosawa type *Anadara-Dosinia* association is found from the horizon slightly lower than that of the Chikubetsu Fauna (OHARA & KANNO, 1973). This indicates the contemporaneity of the Kadonosawa and the Chikubetsu Faunas.

The occurrence of the offshore molluscan fauna is sporadic when compared with the shallow coastal water associations. The lower middle Miocene nearshore sediments in the Setouchi Province are succeeded by offshore type mudstone containing planktic foraminifera and other oceanic planktons of southern aspect. The mudstone is poor in benthic mollusks. Locally nuculanid bivalves, *Portlandia tokunagai*, *P. watasei*, *Malletia inermis*, *Yoldia sagittaria*, are found in association with *Periploma besshoensis*, *Lucinoma acutilineatum*, *Akebiconcha chitanii* and some other bivalves (e.g., Loc. 11, SHIKAMA & KASE, 1976; Loc. 12, ITOGAWA, 1960). The muddy fauna characterized by *P. tokunagai* and *M. inermis* is found in several other areas of north-central Honshu and Hokkaido. The species composition is strikingly uniform throughout these areas. The same association is also found in the early Miocene deposits and the Asahi and the Sankebetsu Formations in central Hokkaido as noted before. The bathymetric relationship between the *Portlandia* association and the subtropical Kadonosawa Fauna is assumed to be the same as

that seen in the early Miocene faunas. The cold water type *Portlandia* association extended its distribution southward into deep water, transported possibly by the previously mentioned cold water undercurrent. Vertical stratification of warm and cold water masses in the Mizunami area (Loc. 12) is proved by the fact that the warm water nautiloid, *Aturia minoensis*, is preserved in association with cold water benthic mollusks.

In early middle Miocene time, the convergence of warm and cold currents was presumably located in central Hokkaido as indicated by the distribution of two shallow water molluscan faunas. The location is about 8° N of the present-day convergence of the warm Kuroshio and cold Oyashio Currents, which is at about 36° N latitude with seasonal fluctuations, along the Pacific coast of Japan. On the other hand, the middle Miocene undercurrent of cold water probably reached down to central Honshu, about 35° N, as suggested by the distribution of the *P. tokunagai* association, the position approximately the same as today. OKUTANI (1972) noted the reduction of size among the subarctic mollusks which are living in the Oyashio Undercurrent in Sagami Bay, central Honshu. No such phenomenon has been reported for the Miocene deep water species.

MIDDLE MIOCENE FAUNA

Middle Miocene deposits in the Japanese Islands are predominated by offshore mudstone. They are represented by hard diatomaceous shale in the Japan Sea coast areas where the shale has been called the Onnagawa Formation and other local names. The diatomite is thought to have been accumulated in silled and stagnant basins (INGLE & GARRISON, 1976).

Shallow water sediments positively able to be correlated with the middle Miocene mudstone and shale facies are not known. Most of the Japanese Islands are likely to have been submerged in deep quiet waters. The shale as well as clastic mudstone is extremely poor in benthic megafossils. Scattered mollusks including *Portlandia tokunagai*, *Conchochele disjuncta*, *Lucinoma acutilineatum*, and some other bivalves have been reported from the mudstone. The molluscan fauna of this age is very poorly understood.

LATE MIOCENE FAUNAS

The shallow water sediments reappeared in the late Miocene along the marginal parts of the basins and surrounding the newly emerged lands in Northeast Japan and the Japan Sea coast areas. The sediments are rich in molluscan fossils. In the depocenter of the basin, the middle Miocene

shale and mudstone is succeeded by grey siltstone or fine-grained sandstone containing offshore type mollusks. The age of reappearance differs from place to place; the earliest may have been in the middle Miocene, around 12 my ago.

Apparently tropical and subtropical mollusks, which predominated during the early middle Miocene disappeared from Northeast Japan and the Japan Sea coast prior to the late Miocene. The subtropical fauna was restricted to the Pacific coast of Southwest Japan (Figure 4).

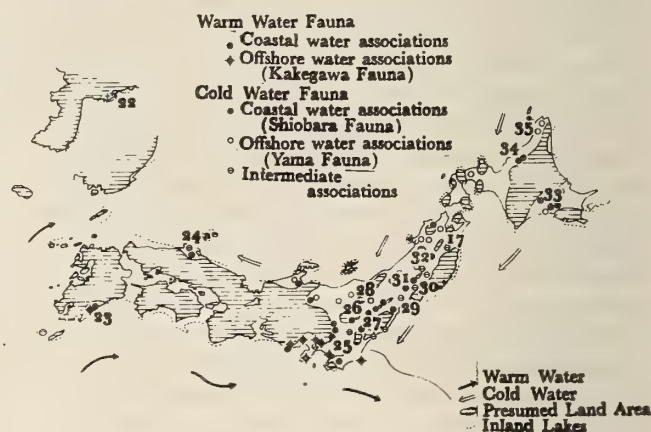


Figure 4

Distribution of the late Miocene molluscan faunas and presumed paleogeography of Japan during the late Miocene. Numerals indicate the fossil localities mentioned in the text: 23: Miyazaki; 24: Fujina in Sanin District; 25: Zushi in the Miura Peninsula; 26: Shiobara; 27: Tanagura; 28: Yama in the Aizu District; 29: Nanakita, north of Sendai; 30: Ichinoseki; 31: Kurikoma; 32: Kurosawa; 33: Atsunai; 34: Togeshita; 35: Wakkanai

The late Miocene subtropical fauna is typically seen in the Miyazaki area (Loc. 23), southern Kyushu. Muddy sandstone of the lower Miyazaki Group contains *Paphia exilis*, *Amussiopecten iitomiensis*, *Crassatellites tenuiliratus*, associated with *Joannisiella cummingi*, *Dosinia* spp., *Cardium* spp., *Clementia* and other bivalves and gastropod species (SHUTO, 1961). The fauna is comparable in generic composition to the Recent inner sublittoral sandy communities of an open coast. The association of outer sublittoral character is found in sandy siltstone of the lower to middle part of the Miyazaki Group. It consists of *Acila submirabilis*, *Limopsis obliqua*, *Glycymeris rotunda*, *Nemocardium samarangae*, *Ancilla otukai*, *Polinices reiniana*, and

some other minority species. No intertidal community is known in the fauna.

The fauna has a close similarity to the Plio-Pleistocene Kakegawa Fauna, which will be discussed later, both in species composition and in distribution. Late Miocene and Plio-Pleistocene faunas both lived in coastal and offshore waters probably affected as today by the warm Kuroshio Current. The differences between them may be attributed simply to their differing geologic ages. They are both called the Kakegawa Fauna in this paper.

In southern Kanto, there is a peculiar assemblage composed of shallow water rocky or gravelly bottom species mixed with offshore deep water forms. The basal conglomerate of the Kazusa Group in the Miura Peninsula (Loc. 25) contains *Chlamys miurensis*, *Amussiopecten iitomiensis*, *Glycymeris cisshuensis*, *Turbo* sp., *Haliotis* sp., associated with *Phanerolepida transenna*, *Mikadotrochus yoshiwarai*, *Halicardia* sp., and other deep water species (SHIKAMA, 1973). Analogous mixed assemblages are found in several localities of the same horizon in Kanto.

Two late Miocene cold water faunas, the nearshore Shiobara Fauna and the offshore Yama Fauna, have been recognized in Northeast Japan and along the Japan Sea coast (CHINZEI, 1963).

The species characteristic of the Shiobara Fauna were first reported from the Shiobara area, central Honshu (Loc. 26) by YOKOYAMA (1926). Composition of the fauna and its relation to habitats in the Tanakura and Shiobara areas were described by IWASAKI (1970). An embayment of late Miocene age has been restored in the Tanakura area (Loc. 27). The horizontal distribution pattern of mollusks in the restored bay is similar to that in the early middle Miocene Kadonosawa Basin. In front of the fresh water sand and lignite areas of the bayhead, there is a belt of banks and colonies of *Crassostrea gigas* with some other species. This represents the tidal flat community. Inside the belt of oyster banks, an area of the *Anadara-Dosinia* association occurs. The association is characterized by high diversity of species and large numbers of individuals. It is dominated by *Anadara ninohensis*, in association with *Dosinia kaneharai*, *Felaniella usta*, *Laevicardium shiobarense*, *Glycymeris cisshuensis*, *Protothaca tateiwai*, other shallow-burrowing bivalves, and with the gastropods *Neverita kiritaniana* and *Phos iwakianus*. The association is equivalent to the *Anadara-Dosinia* association in the Kadonosawa Basin. The main part of the bay is occupied by massive fine-grained sandstone, in which *Lucinoma annulata*, *Macoma optiva*, *Turritella tanaguraensis* are found. This is comparable with the early middle Miocene *Lucinoma-Macoma* association of subtidal muddy bottom. There are small lenses of pumiceous coarse-grained sandstone in the massive sandstone area. The lenses contain a pectinid asso-

ciation consisting of *Mizuhopecten paraplebejus*, *Miyagipecten matsumoriensis*, *Chlamys kaneharai*, with *Glycymeris yessoensis* and a few other species.

The occurrence of *Dosinia kaneharai*, *Laevicardium shiobarense*, and *Chlamys kaneharai* is a characteristic feature of the Shiobara Fauna. The fauna has been reported from the northern margin of the Kanto Basin, and extends farther along the row of islands which was emergent during middle and late Miocene at the position now occupied by the Ou Range. In the Kurikoma area (Loc. 31), central Ou Range, the fauna is characterized by *Spisula kurikoma*, a species common in northern Honshu and Hokkaido, in addition to *Dosinia kaneharai* and *Laevicardium shiobarense*. The same fauna has been called the Togeshita Fauna in Hokkaido, and is known from several areas, e.g., Togeshita (Loc. 34), Atsunai (Loc. 33), in central and eastern Hokkaido (UOZUMI, 1962). In the Sanin district (Loc. 24), western Honshu, the Upper Miocene Fujina Formation, consisting of fine-grained sandstone, contains *Anadara ogawai*, *Dosinia kaneharai*, *Mercenaria yokoyamai*, *Cultellus izumoensis*, and others accompanied by *Nautilus izumoensis*. The fauna, characterized by occurrence of *Anadara ogawai*, *Laevicardium shiobarense*, *Dosinia kaneharai* and other species of the Shiobara Fauna, is known from the upper part of the Miocene Meisen Series in northern Korea (Loc. 22; MAKIYAMA, 1936).

The shallow water type Shiobara Fauna is composed of *Anadara*, *Dosinia*, and other genera derived from the Indo-Pacific region intermingled with such northern species as *Glycymeris yessoensis* and *Spisula kurikoma*, etc. Since there are no apparent warm water species in the fauna, the Shiobara most probably lived in cold water, presumably coastal water in the temperate region. The Indo-Pacific elements may be considered as the descendants of invaders from the south in the early middle Miocene, who remained in the coastal area after the retreat of the warm current and succeeded in adapting themselves to cold water.

The offshore type Yama Fauna was first described by NOMURA (1935) from the Aizu area (Loc. 28). OTUKA (1941) noticed its offshore nature based on an association from the Kurosawa area (Loc. 32). In Hokkaido, the fauna of the same composition is called the Wakkanai Fauna (UOZUMI, 1962). The Yama Fauna is characterized by buccinid and neptuneid gastropods, such as *Ancistrolepis mogamiensis*, *Buccinum ishidae*, *Neptunea nomurai*, and by the cardiid bivalves *Serripes groenlandicus* and *S. yokoyamai*, associated with *Conchocele bisecta* and other bivalves. Analogous associations of species are living in subarctic water in outer sublittoral to upper bathyal zones. Characteristic species of the Yama Fauna are found solitarily or a few species together in grey siltstone accumulated in the basins west of the row of newly emerged

islands. In Hokkaido, it is known from the Wakkanai Shale (Loc. 35) and its equivalents, in which the species of the Yama Fauna are associated with *Portlandia watasei*, *P. thraciaeformis* and others.

The association intermediate in character between the offshore type Yama Fauna and the nearshore Shiobara Fauna is frequently found in fine-grained sandstone distributed between the shallow water sand facies and the deep water mud facies. The fossiliferous Kurosawa Formation in the Kurosawa area (Loc. 32) becomes sandy eastward, closer to an inferred island, where it contains *Macoma optiva*, *Lucinoma acutilineatum*, *Panomya simotomensis*, and *Cultellus izumoensis*, with *Serripes* spp. and a few gastropods (HAYASAKA, 1957). Similar fine-grained sand associations are dominant in the basins east of the row of islands, e.g., Ichinoseki (Loc. 30), Nanakita (Loc. 29), and Kadonosawa areas (Loc. 17). *Miyagipecten matsumoriensis* is another characteristic species of this fine-grained sandstone facies. Conglomeratic sandstone of the same horizon yields a pectinid association characterized by *Mizuhopecten kimurai*, *Kotorapecten yamasakii*, and *K. tryblum* (e.g. LOC. 17, MASUDA, 1962).

PLIOCENE AND EARLY PLEISTOCENE FAUNAS

Structural growth of the Japanese Islands became pronounced during the Pliocene and early Pleistocene, during which time the areas of marine sedimentation were reduced to the coastal belts of the Pacific and Japan Sea. A minor transgression is recognized, however, in Northeast Japan in the late Pliocene. It formed deep embayments in the Pacific side of northern Honshu and central and north Hokkaido. Faunal characters and their distribution during the Pliocene and early Pleistocene were not markedly different from the preceding late Miocene, although some constituent species were replaced by new forms (Figure 5).

A warm water fauna of Pliocene and early Pleistocene age, the Kakegawa Fauna, is distributed along the Pacific coast of Southwest Japan. This fauna comprises associations of diverse habitats, from inner sublittoral to bathyal zones. The fauna is comparable to the living fauna in central and western Japan in the waters associated with the Kuroshio Current. A typical set of the associations is observed in the Kakegawa Group in the Pacific coast of central Honshu (Loc. 37). The Kakegawa area has been studied repeatedly, and faunal characters are best understood here among the distribution areas of the Kakegawa Fauna (e.g., MAKIYAMA, 1931; TSUCHI, 1960).

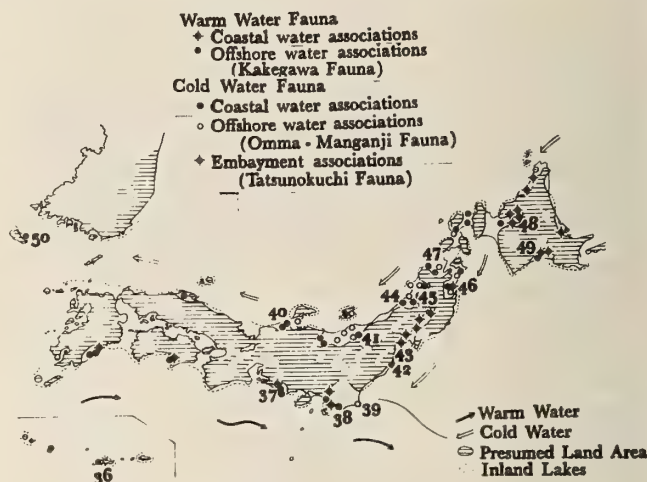


Figure 5

Distribution of the Pliocene and early Pleistocene mollusk faunas and presumed paleogeography of Japan during the Pliocene and early Pleistocene. Numerals indicate the fossil localities mentioned in the text; 36: Shimajiri in Okinawa-jima; 37: Kakegawa; 38: Kurotaki in the Boso Peninsula; 39: Choshi; 40: Omma in Kanazawa; 41: Higashiyama; 42: Futaba; 43: Sendai; 44: Manganji; 45: Futatsui; 46: Sannohe; 47: Tsugaru; 48: Takikawa; 49: Honbetsu; 50: Cheju Island

An inner sublittoral coastal water association is known in the marginal and basal medium-grained sandstone facies of the Kakegawa Group. It is composed mainly of sandy bottom dwellers intermingled with the species from other habitats. The association is characterized by the common occurrence of *Anadara castellata*, *Venericardia panda*, *Amussiopecten praesignis*, *Glycymeris nakamurai*, *Turritella perterebra*, and *Umbonium suchiense*. The species are peculiar to the Kakegawa Fauna, and the occurrence of one of these species is thought to be indicative of the distribution of the fauna.

Lateral change of offshore mollusk fauna corresponding to the lithofacies changes in the Kakegawa Group have been noted by CHINZEI & AOSHIMA (1976). In the offshore area of medium-grained sand, there is a belt of fine-grained muddy sandstone containing outer sublittoral muddy bottom mollusks such as *Venus foveolata*, *Glycymeris rotunda*, *Nemocardium samarangae*, and *Siphonalia spadicea*. The association from the coarse-grained siltstone is dominated by gastropod species, now living in the uppermost bathyal zone, such as *Nassaria magnifica*, *Makiyamaia coreanica*, *Fulgoraria hirasei*, and *Lunatia plicispira*. The offshore

fine-grained siltstone contains scattered *Limopsis tajimae*, a species characteristic of the present-day upper bathyal, associated with *Neilonella coix*, *Malletia inaequilateralis*, and gastropods in common with the coarse-grained siltstone facies.

Associations similar to those in the Kakegawa area are distributed along the Pacific coast of Southwest Japan southward to the Ryukyu Islands. The coastal water associations have not been found on Okinawa-jima and other nearby islands (MACNEIL, 1960). A bathyal molluscan fauna, representing the deepest association among the known Kakegawa Fauna, is reported from Okinawa-jima (Loc. 36, NODA, 1976). It includes *Neilonella japonica*, *Bathyarca sibogai*, *Turricula aeola*, and *Benthovoluta hildendorfi*. The northeastern limit of distribution of the shallow water association is found in the central part of the Boso Peninsula, southern Kanto (Loc. 38).

The Pliocene and Early Pleistocene molluscan fauna of the Japan Sea coast of Honshu has been called the Omma-Manganji Fauna. The general character of the fauna is cold water, composed of species now living in the areas under the influence of the cold Oyashio Current, and by extinct species. Three principal associations are recognized in the Omma-Manganji Fauna: coastal water sandy bottom associations, coastal water gravelly bottom associations, and offshore muddy bottom associations.

The typical composition of the shallow sandy bottom associations was described in the Futatsui area, northern Honshu (Loc. 45, CHINZEI, 1973), where two types of associations are recognized in fine-grained sandstone. The association from the lower horizon is characterized by the predominance of *Limopsis tokaiensis*, *Acila nakazimai*, *Venericardia ferruginea*, and *Turritella saishuensis*. The association presumably lived in deeper water than the overlying *Anadara-Mercenaria* association, as it is found in an intermediate horizon between the offshore muddy association and the *Anadara-Mercenaria* association. The *Anadara-Mercenaria* association, found in the upper horizon, is composed mainly of *Turritella saishuensis*, *Macoma tokyoensis*, *Anadara amacula*, *Mercenaria stimpsoni*, *Dosinia japonica*, *Mya cuneiformis*, *Thracia kakumana*, and *Felaniella usta*.

The fauna in gravel or coarse-grained sandstone is characterized by the common occurrence of *Astarte borealis*, *Glycymeris yessoensis*, *Chlamys cosibensis*, *Epitonium* spp., *Ocenebra* spp., and *Boreotrophon* spp., e.g., in the Manganji area (Loc. 44, OTUKA, 1936) and in the Nishi-Tsugaru area (Loc. 47, IWAI, 1965). It is usually intermingled with the species probably derived from other facies.

These associations are found separately, or intermingled with each other, in Pliocene and lower Pleistocene sandy sediments in many other areas along the Japan Sea coast. In the Omma area near Kanazawa (Loc. 40), one of the typical localities of the fauna, fossils are found as shell beds composed mainly of the species in common with, or closely related to, those in the Futatsui area. They are intermixed with those from other facies (OGASAWARA, 1977). There are some indigenous species such as *Mizuhopecten tokyoensis hokurikuensis*, *Anadara ommaensis*, and *Pseudamiantis tauyensis*.

The offshore muddy fauna in the Futatsui area is represented by *Nuculana robai*, *Macoma calcarea*, *Serripes groenlandica*, *Conchocele bisecta*, *Turritella nipponica*, *Buccinum tsubai*, and *Rectiplanes sadoensis* (CHINZEI, 1973). These species are found sporadically in grey siltstone. In general, the offshore muddy association in the Omma-Manganji Fauna is characterized by the dominance of gastropods such as *Admete*, *Antiplanes*, *Propebela*, and other buccinid and turrid species.

As the Pliocene and the lower Pleistocene strata on the Japan Sea coast areas were accumulated at the last stage of reclamation of the Neogene basins, the offshore fauna tends to occur in the lower horizon, and is replaced upward by the shallow water associations as observed in the Futatsui area. The age of appearance of the shallow water association may differ in places, it is earlier in the marginal areas and later in the central parts of the basin.

The westernmost distribution of the Omma-Manganji Fauna is on Cheju (Saishu) Island (Loc. 50), southern Korea, from which *Turritella saishuensis* was described by YOKOYAMA (1923). In this locality, *T. saishuensis* is associated with *Venericardia ferruginea*, *Chlamys cosibensis*, *Mizuhopecten tokyoensis*, and some other mollusks. No further information is available on the fauna associated with *T. saishuensis* on Cheju Island. The distribution of the Omma-Manganji Fauna is thought to be confined to the Japan Sea coast area. However, shallow sandy mollusks from the Futaba area (Loc. 42), south of Sendai, may be referred to the Omma-Manganji Fauna (HAYASAKA, 1956). Also, an offshore muddy association similar to that in the Omma-Manganji Fauna is recorded in the Choshi area (Loc. 39), eastern Kanto (OZAKI, 1958).

It should be noted that the elements of the warm Kakegawa Fauna, *Glycymeris nakamura* and *Umbonium suchiense*, were reported in association with the Omma-Manganji shallow water sandy mollusks from the Higashiyama area, Niigata Oil Field (Loc. 41, KANEHARA, 1940). Occurrence of the warm water Kakegawa elements on the Japan Sea coast of central Honshu indicate a marine connection with the Pacific side.

The embayments formed during the minor late Pliocene transgression were inhabited by a fauna of brackish and shallow marine aspect. The fauna, called the Tatsunokuchi (Tatunokuti) Fauna, is characterized by bivalve species indigenous to these embayments, particularly by a hump-backed pectinid, *Fortipecten*. It is typically found in the Sendai Basin (Locs. 30 and 43), and is known from the Sannohe area in northern Honshu (Loc. 46), and the Takikawa (Loc. 48), Honbetsu (Loc. 49) and other areas in northern and eastern Hokkaido. In the Sendai basin, *Fortipecten takahashii* is found in poorly sorted medium- to coarse-grained sandstone in association with *Pseudamiantis sendaicus*, *Anadara tatunokutiensis*, *Dosinia tatunokutiensis*, *Peronidia* sp., *Neverita kiritaniana*, and other species. Although the association represents the Tatsunokuchi Fauna, it is found in restricted parts of the restored bay (CHINZEI & IWASAKI, 1967). The inner half of the deep embayment is an area of dark grey sandy siltstone, in which large banks of *Crassostrea gigas* are predominant; the cen-

tral part of the bay is occupied by a *Macoma-Mya* association composed of *Macoma tokyoensis*, *Mya japonica*, and *Lucinoma annulata*, found sporadically in grey massive siltstone (Figure 6).

The shallow water association in the Sannohe area (Loc. 46) is peculiar in the combined occurrence of the Tatsunokuchian and Omma - Manganjian species (CHINZEI, 1961). The association from poorly sorted medium-grained sandstone is characterized by *Anadara tatunokutiensis*, *Peronidia protovenulosa*, *Mercenaria stimpsoni*, *Spisula kurikoma*, and *Fortipecten kenyoshiensis*. An offshore muddy association of the Omma-Manganji type is found in the central and deeper part of the Sannohe Basin. *Fortipecten takahashii* is associated with *Turritella fortilirata*, *Spisula voyi*, *Macoma tokyoensis*, *Yoldia macroshema*, *Anadara "trilineata"*, and *Mya japonica* in the Takikawa area (Loc. 48), central Hokkaido. The fauna is found in the innermost part of the embayment. The association characterized by *Fortipecten takahashii* is commonly found in the Plio-Pleistocene sandy facies of northern and eastern Hokkaido.

The shallow sandy association of *Fortipecten takahashii* is dominated by *Anadara*, *Dosinia*, *Peronidia*, and *Pseudamiantis* or *Mercenaria* in the Sendai and other areas. The principal generic composition is comparable to that of the shallow sandy association of the Omma-Manganji Fauna in Futatsui and other areas, although there are no species in common. The *Anadara-Dosinia* association of the Tatsunokuchi and the Omma-Manganji faunas occupied a similar biotope in the different basins, but they are thought to have been separated zoogeographically from each other.

MOLLUSCAN ASSOCIATIONS

- △ *Batillaria*
- *Crassostrea*
- ◆ *Pseudamiantis - Anadara*
- *Felaniella*
- *Macoma - Mya*

LITHOFACIES

- ▬ Grey mud
- ▬ Black mud
- ▬ Muddy sand
- ▬ Gravel



Figure 6

Distribution of the coastal water associations in the late Pliocene embayment of the Sendai Basin. Thick line indicates the presumed coastline. Locality 30: Ichinoseki; Locality 43: Sendai. Redrawn from CHINZEI & IWASAKI (1967)

PALEOECOLOGICAL NOTES ON THE JAPANESE NEOGENE MOLLUSCAN FAUNAS

Most associations represent original species associations. This is confirmed by observations of autochthonous fossil occurrences, i.e., individuals that lived together and were buried at their living places. Some other associations do not show positive evidence of *in situ* preservation, but identical species associations have been reported from many localities. Their compositional identity suggests that the observed species composition is original. Such an association represents part of the original benthic community in the sense of PETERSEN (1913).

Similarity of species composition is remarkable among the shallow water associations of different ages, especially among those of the embayments (Figure 7). Associations characterized by potamid gastropods and oysters of the genus *Crassostrea* are known from all 4 faunas of different

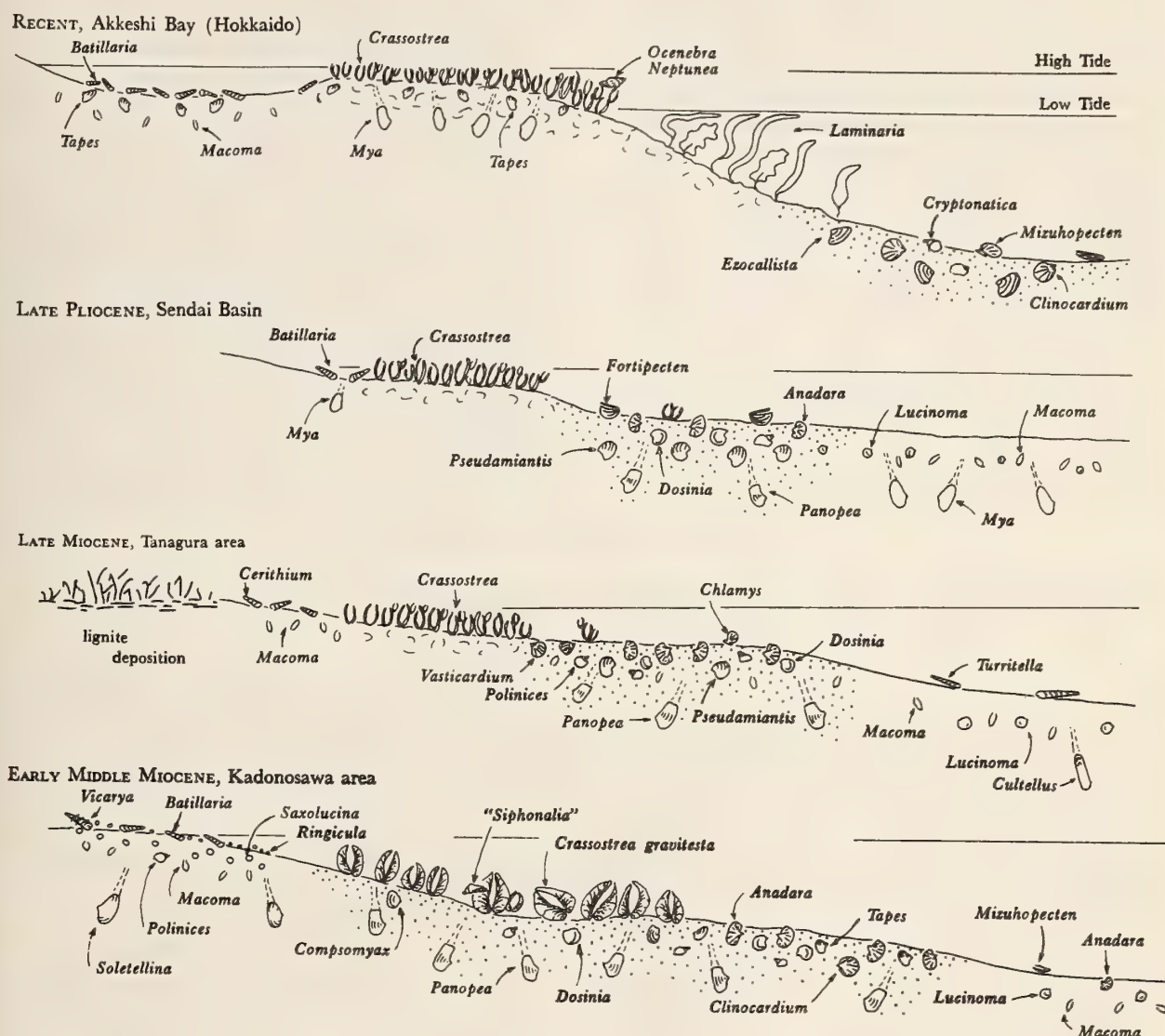


Figure 7

Coastal water molluscan associations of the early middle Miocene Kadonosawa Fauna (Kadonosawa Basin, Locality 17), the late Miocene Shiobara Fauna (Tanagura area, Locality 27), and the Pliocene Tatsunokuchi Fauna (Sendai Basin, Locality 43). Recent cold water associations in Akkeshi Bay and adjoining brackish water Akkeshi Lake, eastern Hokkaido, are also shown for comparison.

ages. They are found invariably in mud or muddy sand of the marginal part of a sedimentary basin or the innermost

part of an embayment. They may represent intertidal communities. Shallow water sandy facies were populated by associations dominated by *Dosinia*, *Anadara*, *Cardium* and other shallow-burrowing suspension feeders. They are commonly associated with carnivorous naticid gastropods. The species diversity as well as population density in this facies are the highest of all of the Neogene molluscan associations. The high proportion of burrowing suspension feeders corresponds with that of the present-day sandy bottom fauna (SANDERS, 1958; KIKUCHI, 1977). The shallow muddy bottom associations are dominated by *Macoma* and

Lucinoma in common besides other species peculiar to each association. They are rich in deposit feeding forms. Naticids are uncommon in these associations. Table 1 shows a comparison of the principal constituents of representative shallow water and embayment associations.

These similarities of composition are indicative of analogous ecologic characters of the associations. The ecologically congruent relationships of the associations were first discussed by CHINZEI & IWASAKI (1967) for the shallow sea faunas in northern Honshu. They called the relationship chronologically parallel comparing it with geographically parallel ones seen in the Recent benthic communities (THORSON, 1957). Congruent relationships are not clear among the offshore associations in the Japanese Neogene.

Species are usually replaced, between the congruent

associations of different ages, by different species belonging to the same genus or ecologically allied genera. The replacement of species may be the consequence of evolutionary change within the same genus, as well as new immigration from the south to the north. For example, species of *Anadara* that lived in Northeast Japan from the late Miocene through the early Pleistocene are probably the descendants of species that invaded Japanese waters from the south during early middle Miocene time. The species found in the Kakegawa Fauna, however, is considered to be an immigrant from the south during Pliocene. The coastal water mollusks living in present-day Japanese waters may be the descendants of species that lived in coastal waters during Neogene and partly species that immigrated from the south during the late Pleistocene and post-glacial ages.

Table 1

Species composition of representative coastal water associations in the Neogene molluscan faunas in Japan. Note the occurrence of the same or ecologically allied species among the associations of different ages.

Age (Example)	Early Miocene (Loc. 2, Kottoi; subtropical)	Early Middle Miocene (Loc. 17, Kadonosawa; subtropical) *(Loc. 12, Mizunami)	Late Miocene (Loc. 27, Tanagura; temperate)	Pliocene— Early Pleistocene (Loc. 43, Sendai; temperate)	Living (Akkeshi, Hokkaido; cold temperate)
Presumed Environment					
Tidal flat (muddy sand or sandy mud facies)	<i>Batillaria takeharai</i>	<i>Batillaria yamanarii</i> <i>Vicarya callosa japonica</i> <i>Macoma cf. incongrua</i> <i>Soletellina minoensis</i> <i>Cyclina japonica</i>	<i>Cerithium kobelti</i> <i>Macoma incongrua</i>	<i>Batillaria multiformis</i> <i>Macoma incongrua</i> <i>Mya japonica</i>	<i>Batillaria cumingi</i> <i>Macoma incongrua</i> <i>Mya japonica</i> <i>Tapes japonica</i>
Intertidal (muddy or sandy facies)	<i>Crassostrea</i> sp.	<i>Crassostrea gravitesta</i> <i>Compsomyx iizukai</i> <i>Panopea kanomataza- waensis</i>	<i>Crassostrea gigas</i>	<i>Crassostrea gigas</i>	<i>Crassostrea gigas</i> <i>Tapes japonica</i> <i>Mya japonica</i>
Level bottom (sandy facies)	<i>Dosinia chikuzenensis</i> <i>Glycymeris cisshuensis</i> <i>Pitar matsumotoi</i> <i>Sollen connectens</i> <i>Solen connectens</i>	<i>Dosinia nomurai</i> <i>Glycymeris cisshuensis</i> <i>Tapes siratoriensis</i> <i>Compsomyx iizukai</i> <i>Anadara ninohensis</i> <i>Clinocardium shinjiense</i> <i>Panopea kanomataza- waensis</i> <i>Euspira meisensis</i>	<i>Dosinia kaneharai</i> <i>D. japonica</i> <i>Glycymeris cisshuensis</i> <i>Protothaca lateiwa</i> <i>Pseudamiantis pinguis</i> <i>Mercenaria yokyamai</i> <i>Anadara ninohensis</i> <i>Laevicardium shioba- rense</i> <i>Panopea japonica</i> <i>Neverita kiritaniana</i>	<i>Disinia tatunokutiensis</i> <i>Glycymeris gorokuensis</i> <i>Pseudamiantis sendaicus</i> <i>Anadara tatunokutiensis</i> <i>Clinocardium pseudo- fastosum</i> <i>Panopea japonica</i> <i>Neverita kiritaniana</i>	<i>Glycymeris yessoensis</i> <i>Ezocallista brevisiphonata</i> <i>Clinocardium californiense</i> <i>Cryptonatica janthostoma</i>
Level bottom (muddy facies)	<i>Angulus maximus</i> <i>Venericardia subnipo- ponica</i> <i>Cultellus izumoensis</i>	* <i>Macoma optiva</i> <i>Venericardia siogam- ensis</i> <i>Lucinoma acutilineatum</i> <i>Cultellus izumoensis</i>	<i>Macoma optiva</i> <i>Lucinoma annulatum</i> <i>Cultellus izumoensis</i>	<i>Macoma tokyoensis</i> <i>Lucinoma annulatum</i>	

SUMMARY

OF ZOOGEOGRAPHIC CHANGES

OF THE JAPANESE ISLANDS

DURING NEOGENE AS VIEWED

FROM BENTHIC MOLLUSKS

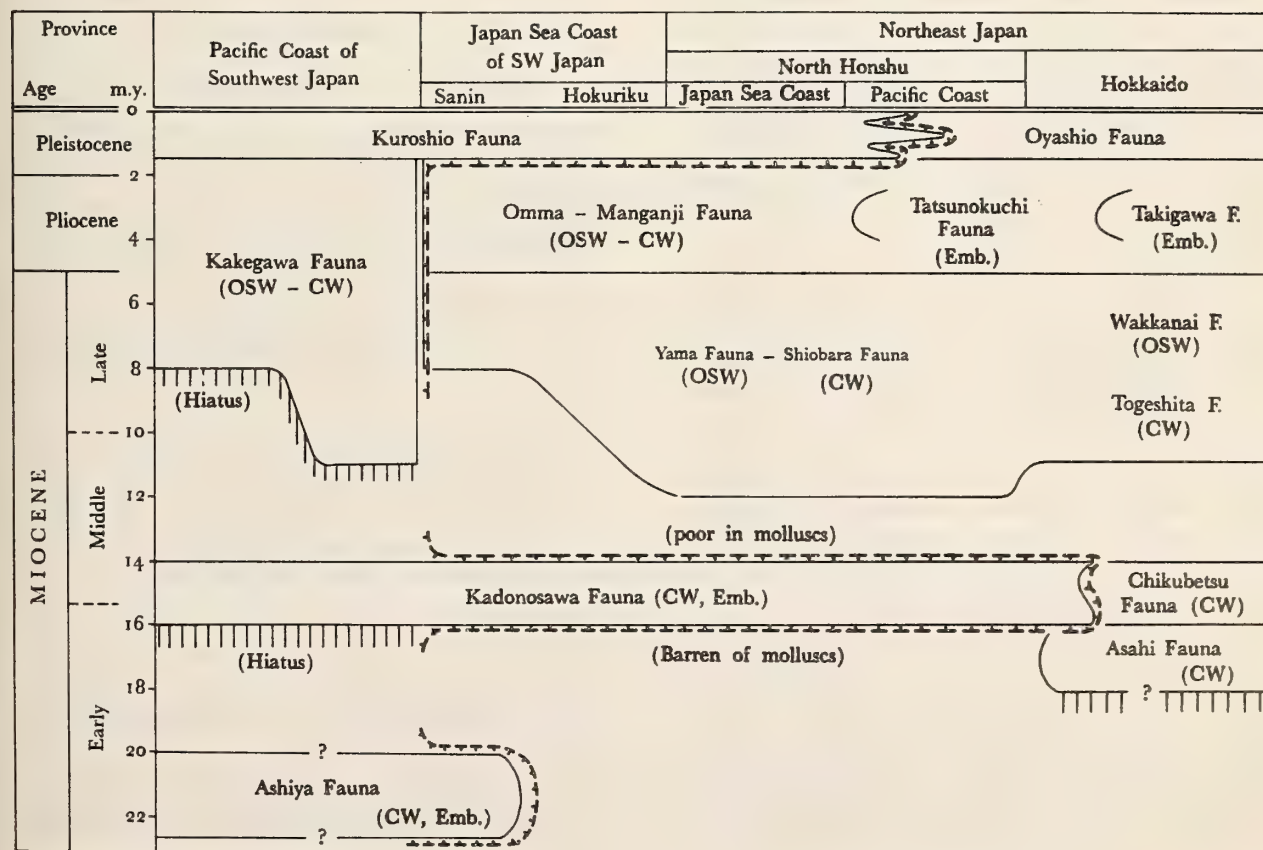
Distributions of the Neogene molluscan faunas in space and time are summarized in Figure 8. The boundaries of the faunas are greatly simplified, and the chronologic positions of the early Miocene faunas are tentative.

The predominance of warm water faunas in early middle Miocene time is the most pronounced event in the faunal history of the Japanese Neogene mollusks. At this time the convergence between warm and cold currents, the subtropical front, was most probably located as far north as central Hokkaido. A major part of Japan was inhabited by the tropical and subtropical coastal water faunas. The main stream of the warm water current probably passed along

the Japan Sea side of the Islands, because the tropical mollusks are known only from the Japan Sea coast and adjoining areas in western Japan. The vertical structure of water masses in the early middle Miocene was possibly different from that of present-day Japanese waters. The undercurrent of cold water reached down to central Honshu along the Pacific coast, approximately at the same position as today. Perhaps the early middle Miocene warm surface current in the area now constituting Japan was thinner than the present Kuroshio Current, thus allowing a deep, cold water tongue to advance far south of and beneath the subtropical front.

Figure 8
(below)

Chronologic and geographic distributions of the Japanese Neogene and Pleistocene molluscan faunas. osw: offshore water associations; cw: coastal water associations; emb: embayment and brackish water associations.



Limit of tropical-subtropical faunas

Duration of pronounced warming was probably short, around 1 or 2 my, apparently within Blow's planktic foraminiferal Zones N8 and Ng. The beginning of the warm period is uncertain. It might have been contemporaneous with the start of the middle Miocene transgression. Data are too scanty to obtain a clear image of zoogeography during the early Miocene, and the transition from the early Miocene faunas to those of early middle Miocene is obscure.

The early middle Miocene period of warming has been recorded from the northern and eastern coast of the Pacific (e.g., ALLISON, 1976; ADDICOTT, 1969), as well as from the South Pacific (HORNIBROOK, 1977) and from the Antarctic Sea (SHACKLETON & KENNETT, 1975). This indicates that the faunal episode in Japan was induced by global activation of warm current systems.

The end of the warm period is seemingly abrupt as far as the benthic faunas are concerned. In the late Miocene no apparent subtropical species has been reported from the entire Japan Sea coast area. The late Miocene faunas in the Japan Sea areas are composed exclusively of the cold water species, elements of the subarctic and coastal waters of the temperate region. This is a sharp contrast to the tropical or subtropical nature of the early middle Miocene faunas in these areas. The switchover from warm to cold water happened during the middle Miocene, around 14 my ago, as revealed by an abrupt change of benthic foraminiferal fauna in the Japan Sea areas (e.g., TAI, 1963; MAIYA, 1977). TAI (1963: 4) called the horizon of change as "Foram. Sharp Line." The sharp change in the Japan Sea area might be the result of closure of the Korean Strait, rather than abrupt global change of climate.

The benthic molluscan faunas in the Japan Sea areas have maintained their cold water nature from the late Miocene through the beginning of the early Pleistocene. Apparent warm water species reappeared in the Japan Sea areas during the early Pleistocene and later as exemplified by the occurrence of *Conus* and other warm water species from the upper part of the Omma Formation (OGASAWARA, 1977). KOIZUMI (1977) noted the occurrence of a warm water diatom flora in the late Miocene from a piston-core sample obtained in the central part of the Japan Sea. He considered that the Sea was connected with the Pacific both to the south and to the north. The only indication of this warming found on land is the occurrence of *Nautilus izumoensis* in the upper Miocene of the Sanin area (Loc. 24) and a few other localities.

The convergence of cold and warm waters in the late Miocene was probably located in Kanto, central Honshu, at approximately the same position as today. After this, no marked shift of the position of convergence is detected through the molluscan faunal sequence. The convergence

has remained relatively stationary during the late Neogene and the early Pleistocene. Oxygen paleotemperature analysis shows that the thermal structure of the warm water in Plio-Pleistocene time was comparable to that of the present-day Kuroshio and associated water (CHINZEI & AOSHIMA, 1976).

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Professor Tetsuro Hanai and my colleagues in the University of Tokyo, and Dr. Yasuhide Iwasaki of Kumamoto University gave valuable suggestions and advice on various aspects of paleontologic problems. Comments on the biogeography and ecology of present Japanese waters were made mainly by Professor Masuoki Horikoshi of the University of Tokyo. Discussions with many other friends were also stimulating for me. The manuscript was reviewed by Dr. Warren O. Addicott of U. S. Geological Survey, Menlo Park, Professor T. Hanai, and Dr. J. A. Grant-Mackie of the University of Auckland, New Zealand. My deep appreciation is due to these persons for their kind help.

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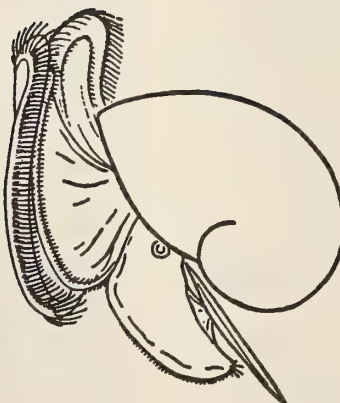
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Late Oligocene Through Pleistocene Molluscan Faunas in the Gulf of Alaska Region

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(2 Text figures)

INTRODUCTION

A NUMBER OF GULF OF ALASKA Tertiary formations contain fossil faunas of major importance to studies of North Pacific molluscan biostratigraphy and paleobiogeography (Figure 1). These faunas are, however, very poorly known. The interpretations offered here are based on faunal lists for each formation, but available space prohibits their inclusion in this paper. It is my purpose to give a review of 9 Gulf of Alaska stratigraphic units and their molluscan faunas.

I have treated these stratigraphic units and their faunas under "western Gulf of Alaska" and "northeastern Gulf of Alaska" headings because of significant differences in the faunas and geologic history of these two areas during Neogene time. The discussion deals primarily with the Neogene units of the Gulf of Alaska region, although two units, the Sitkinak Island Narrow Cape Formation, and the Poul Creek Formation, range down into the Paleogene. Quaternary marine deposits are also considered.

These North Pacific molluscan faunas are substantially different from those of the European stratotypes, a factor which makes epoch assignments difficult.

I have attempted to correlate the Gulf of Alaska stratigraphic units with the provincial molluscan chronology of the Pacific Northwest Molluscan Province (ARMENTROUT, 1975; ADDICOTT, 1976), or with the late Pliocene to early Pleistocene marine transgressions of Beringia (HOPKINS, 1967). The Pacific Northwest molluscan stages have been correlated with the benthic foraminifer stages of California, which have in turn been loosely correlated with the modern planktonic foraminifer zones by BERGGREN & VAN COUVERING (1974). By this attenuated series of correlations I have attempted to recognize epoch boundaries in the Gulf of Alaska region. I expect substantial refinement of these correlations to result from future studies of western

North American Cenozoic strata. Future research should permit definition of provincial molluscan stages for the Gulf of Alaska region, but present knowledge is insufficient for this purpose, even though a provincial chronology is needed.

In the section that follows, I have given an abbreviated discussion of each Gulf of Alaska stratigraphic unit of late Paleogene to Recent age that bears a significant molluscan fauna. Not all Paleogene or Neogene formations of the area have been discussed. I have attempted to date each unit discussed, and have also offered inferences on water depths and sea temperatures as well as comments on the biogeographic affinities or faunal compositions for the mollusks. My use of European series/epoch terms is in the sense of BERGGREN & VAN COUVERING (1974).

WESTERN GULF OF ALASKA STRATIGRAPHIC UNITS

The Narrow Cape Formation of Sitkinak Island:

Approximately 210 meters of marine fossiliferous siltstone crop out at the axis of a syncline located at the southernmost tip of Sitkinak Island, Alaska. These strata, which were referred to the Narrow Cape Formation by MOORE (1969), conformably overlie the coal-bearing terrestrial Sitkinak Formation of MOORE (1969). Sitkinak Island Narrow Cape Formation strata may be given a new formational name in the future because they differ from the type Narrow Cape Formation strata of Kodiak Island in being gradationally conformable upon the underlying Sitkinak Formation, and in being older, as well as in lacking outcrop continuity. Moore (personal communication, 1976), however, believes that these beds may represent the beginning of the same marine transgression that is represented at Narrow Cape on Kodiak Island, and that the two stratal se-

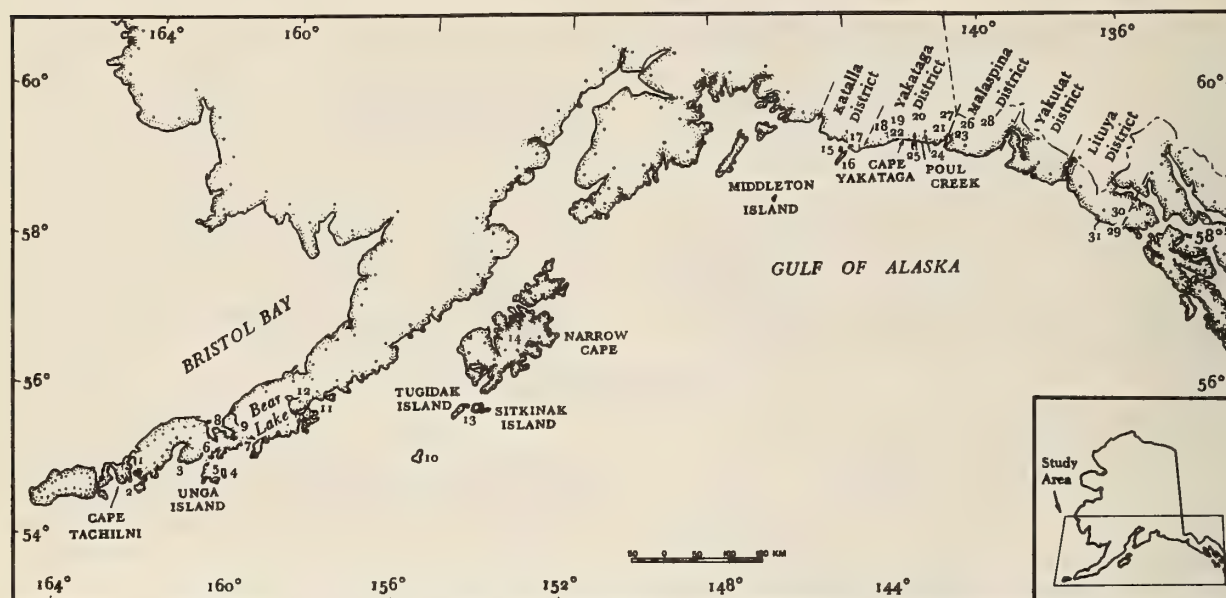


Figure 1

Index Map of the Gulf of Alaska Region Showing Locations of
Major Mollusk-Bearing Stratigraphic Units and the Geographic
Locations of Places Referred to in the Text

- | | | | |
|-------------------|---------------------|------------------------|------------------------|
| 1. Cold Bay | 9. Milky River | 17. Suckling Hills | 25. Yakataga Glacier |
| 2. Thinpoint Cove | 10. Chirikof Island | 18. Grindle Hills | 26. Samovar Hills |
| 3. Coal Bay | 11. Chignik Bay | 19. Kosakuts River | 27. Karr Hills |
| 4. Popof Island | 12. Black Peak | 20. Robinson Mountains | 28. Pinnacle Hills |
| 5. Zachary Bay | 13. Trinity Islands | 21. Guyot Glacier | 29. Icy Point |
| 6. Cape Aliaksin | 14. Kodiak Island | 22. Kulthieth Mountain | 30. La Perouse Glacier |
| 7. Stepovak Bay | 15. Wingham Island | 23. Chaix Hills | 31. Topsy Creek |
| 8. Port Moller | 16. Kayak Island | 24. Munday Peak | |

quences should therefore be referred to the same formational unit. Perhaps future knowledge of the offshore subsurface stratigraphy will clarify this point.

To date, no faunal list has been published for the marine strata which crop out along the south coast of Sitkinak Island, but they contain a molluscan fauna now known from collections made by George Moore of the U.S. Geological Survey and by John Armentrout of Mobil Oil Company. This fauna, which consists of about 55 taxa, is not as diverse as that of the type Narrow Cape Formation of Kodiak Island.

The Sitkinak marine strata belong to the Juanian Stage (ADDICOTT, 1976) [= *Echinophoria apta* zone of DURHAM, 1944] of the provincial molluscan chronology (MACNEIL, 1965: 69). Assignment of these strata to the *Echinophoria apta* zone is confirmed by the presence of the zonal index fossil, *E. apta*. The *E. apta* zone corresponds to the upper

Zemotriian benthic foraminiferal Stage (DURHAM, 1944; ARMENTROUT, 1975; ADDICOTT, 1976). Several taxa which indicate that the Sitkinak marine strata are no older than the Juanian or *E. apta* zone are: *Macoma calcarea* (Gmelin), *Macoma incongrua* (von Martens) of KANNO (1971), *Pitar angustifrons* (Conrad), *Spisula albaria* (Conrad), subsp.?, *Spisula* cf. *S. hannibali* (Clark & Arnold), *Natica clausa* (Broderip & Sowerby), and *Polinices* cf. *P. galianoi* Dall.

Taxa not known to occur in strata younger than those of the *E. apta* zone also occur in the Sitkinak marine strata. These taxa are: *Spisula* cf. *S. hannibali*, *Brucarkia* cf. *B. andersoni* (Wiedey), *Polinices ramonensis* (Clark), and *Priscofusus* aff. *P. stewarti* (Tegland).

BERGGREN & VAN COUVERING (1974) suggest that the late Zemotriian is approximately equivalent to planktonic foraminifer zones N₂/P₂₁ through N₄. If so, the Oligocene-

Miocene boundary may fall high within the *Echinophoria apta* zone, more or less equivalent to the usage of West Coast benthic foraminifer workers. The early Miocene Pillarian molluscan Stage (early Saucian benthic foraminifer Stage) (Figure 2) is unrepresented in the known surface exposures of the western Gulf of Alaska.

A few diagnostic taxa suggest that the Sitkinak Island Narrow Cape Formation strata were deposited in water no shallower than 18 m, and possibly no shallower than 37 m, and probably no deeper than 186 m or possibly no deeper than about 141 m. Kristin McDougall, of the U.S. Geological Survey (personal communication, Sept. 1976) reports the benthic foraminifers from this section to indicate probable depths between 100 and 300 m. Taken together, the evidence suggests water depths during deposition were primarily in the outer neritic depth zone between 100 and 186 m.

Water temperature during deposition of the late Oligocene Sitkinak Island Narrow Cape Formation was clearly temperate and cooler than that of the Miocene Narrow Cape Formation of Kodiak Island. Whether the water temperature was cool temperate like the present Aleutian-Gulf of Alaska region (HALL, 1964), or mild temperate like the present Oregonian province, is more difficult to assess. Both warmer and cooler faunal elements are present. In general, it seems probable that water temperature was slightly warmer than present water temperature at Sitkinak Island, perhaps somewhat like that near the present cool temperate-mild temperate boundary.

The fauna of the Sitkinak Island Narrow Cape Formation contrasts strongly with that of the Narrow Cape Formation of Kodiak Island. The presence of large *Dosinia*, *Securella*, *Anadara* (*Anadara*), large fulgorarids, and *Ficus* at Narrow Cape indicates substantially warmer water conditions, probably like those of the present warm temperate province.

The Sitkinak Island Narrow Cape Formation mollusks are divided among stocks that had their principal centers of distribution, or regions of origin, along the Asiatic coast, along the Pacific Coast of North America, or to a lesser extent in the higher latitude northern perimeter endemic region of the North Pacific. Of the 37 taxa which are amenable to this type of analysis, those with primary Asiatic affinities account for about 32%. Taxa with western North American affinities account for about 35% of the fauna, and species of endemic North Pacific origin account for about 30%. Fourteen percent of the fauna (included with the endemics) is composed of precursors of taxa that later achieved circumboreal distributions. A cosmopolitan species, *Hiattella arctica* (Linnaeus), that forms 3% of the fauna, is the most abundant element in the collections.

The Narrow Cape Formation:

Richly fossiliferous sandstones, siltstones, and conglomerates which crop out along the headland of Narrow Cape on the east side of Kodiak Island have been named the Narrow Cape Formation by MOORE (1969). The formation rests with prominent angular unconformity on the Eocene and Oligocene Sitkalidak Formation. MACNEIL (1965), MOORE (1969), PLAFKER (1971), WAGNER (1974), and ALLISON & ADDICOTT (1973, 1976) have all referred these strata to the provincial middle Miocene.

The megainvertebrate fauna of the Narrow Cape Formation is poorly known, but consists of at least 80 taxa. Fossil collections have been made by the writer and Carol Wagner Allison in 1969, and by W. O. Addicott, J. Wyatt Durham, Saburo Kanno, and the writer in 1970.

The Narrow Cape Formation belongs to the Newportian Stage (ADDICOTT, 1976; ALLISON, 1976). *Mytilus middendorffi* Grewingk, which is restricted to the Newportian Stage (ALLISON & ADDICOTT, 1976), ranges throughout the Narrow Cape Formation. The Newportian Stage is equivalent to the upper Saucian to the Luisian Stages of the West Coast benthic foraminiferal chronology (ALLISON & ADDICOTT, 1976), an interval that BERGGREN & VAN COUVERING (1974) refer to the late early to early middle Miocene. This age assignment is also confirmed by the known ranges of other molluscan taxa.

The molluscan fauna of the Narrow Cape Formation suggests that deposition occurred within the neritic zone. In the lower coarser-grained portion of the formation, a number of beds are composed primarily of molluscan shells and shell detritus. These shell beds contain abundant *Pseudocardium* and *Mytilus middendorffi*, both with heavy valves, well adapted to wave surge in the inner neritic and shallow subtidal environments. These richly fossiliferous beds may be storm concentrations of shell material. *Kewia kannoi* Wagner is also found here, and is thought to indicate an inner neritic environment.

The upper part of the Narrow Cape Formation is composed of finer-grained more massive sandstone and siltstone, and lacks the prominent shell beds. Fossils are sporadic here; these strata appear to have been deposited in slightly deeper water than existed during deposition of the lower part of the formation. Water depth appears to have been within the outer neritic depth zone and no deeper than about 130 m.

Molluscan assemblages of the Narrow Cape Formation indicate warm water conditions within the warm temperate climatic belt of HALL (1964). Cooler water genera, whose members are not found living in water warmer than the warm temperate zone include *Acila*, *Clinocardium*,

Cyclocardia, *Mya*, *Colus*, and *Cryptonatica*. Warm-water genera which presently live in water no cooler than the warm temperate zone include *Anadara*, *Chione*, and *Dosinia*. The presence of the gastropod *Ficus*, which appears to be limited today to the inner and outer tropics, is one of the most convincing indicators of warm water conditions. The Narrow Cape fauna appears to represent the warmest water conditions known among the Oligocene to Recent faunas of the Gulf of Alaska region. ADDICOTT (1969) has discussed this Neogene warm water maximum and its effect on the latitudinal range of *Dosinia* and *Ficus*.

Although the full faunal composition of the Narrow Cape Formation is not yet known, both western North American and Asiatic faunal affinities are apparent. Of the 30 taxa analyzed here, approximately 53% have western North American affinities, about 33% have Asiatic affinities, and about 13% are endemic to the high latitude North Pacific perimeter. One species, *Natica* cf. *N. clausa* (Brodierip & Sowerby), (3% of the fauna; included with the endemics) is a precursor of the living circumboreal species.

The Narrow Cape fauna is also notable in that it is different from the contemporary fauna of the lowermost mainland Yakataga Formation in the Yakataga district. In contrast to the Narrow Cape fauna, the Yakataga fauna is a cool-water fauna showing substantial endemism and relationship to the modern cool-water fauna of the Gulf of Alaska. This fact has hindered detailed correlation between the two faunas.

Unga Conglomerate Member of the Bear Lake Formation:

The name "Unga Conglomerate" was proposed by DALL & HARRIS (1892: 234) for brown conglomerates which overlies coal-bearing strata on Unga Island, Alaska. BURK (1965: 92-93) referred to the Unga Conglomerate as a member of his Bear Lake Formation and designated the type section to consist of all the strata exposed west of Zachary Bay. Thus his 244 m thick measured section of the type Unga Conglomerate Member west of Zachary Bay (BURK, 1965: 212) includes not only the coarse conglomerate of Dall and Harris's Unga Conglomerate, but several hundred feet of underlying sandstone, conglomerate, and lignitic leaf-bearing siltstone. The base of the Unga Conglomerate was considered by Burk to be the unconformity between the underlying Stepovak Formation and the lignitic beds; unfortunately, this contact is not exposed at the type locality of the Unga Conglomerate.

The age of the Unga Conglomerate is difficult to determine because diagnostic fossils are rare, but much confusion also stems from mis-allocation of fossil localities and mixing of fossil collections made in the 1800's. Further

complications have arisen from the widely reported occurrence of *Mytilus middendorffi* in the coarse clastics of the Unga Conglomerate (ALLISON & ADDICOTT, 1976); although this species is correctly considered to be a provincial middle Miocene (Newportian-Temblor) index species, the Unga Conglomerate *Mytilus* is in fact different, and has been described as *Mytilus gratacapi* Allison & Addicott. MACNEIL (1973) has presented the most inclusive account of Unga Conglomerate fossil mollusks.

Analysis of the known stratigraphic ranges of the few taxa identified suggests that the marine beds of the Unga Conglomerate are no younger than early Wishkahan and no older than late Newportian (Figure 2). All the molluscan taxa reported from the Unga Conglomerate, with the exception of the questionably identified *Epitonium* cf. *E. clallamense* Durham, are compatible with, or restricted to, some part of the Newportian to Wishkahan interval. Only two species, *?Sanguinolaria ochotica* Slodkevich, and *Epitonium* cf. *E. howei* Durham, would indicate restriction to the Wishkahan Stage alone; both taxa are doubtfully identified and weak bases for correlation. Three species indicate an age no younger than Newportian: *?Colus kurodai* (Kanehara), of HIRAYAMA (1955) (see MACNEIL, 1973), possibly *Ocenebra topangensis* Arnold, and *Cyclocardia* cf. *C. kevetscheveemensis* (Slodkevich) (seems to indicate only a late Newportian age). The view that *Mytilus gratacapi* descended from the Newportian *Mytilus middendorffi* (ALLISON & ADDICOTT, 1976) is compatible with a late Newportian age for the Unga Conglomerate Member. Although the evidence favors the late Newportian age, an early Wishkahan age cannot be totally excluded.

The leaf-bearing non-marine beds, which belong to the Seldovian Stage (WOLFE in BURK, 1965: 234) are probably not younger than Newportian but could be older (the Homerian-Seldovian Stage boundary is about 12.5 m.y.: personal communication, J. A. Wolfe, Jan., 1976). The presence of Seldovian plant fossils in the Stepovak Formation at Coal Bay (WOLFE in BURK, 1965: 88, 233, 234) suggests that these lowermost non-marine strata may be more reasonably referred to the Stepovak Formation.

The Narrow Cape Formation may be partially coeval with the Unga Conglomerate Member, or may be wholly older. The Unga Conglomerate Member appears to be of latest early to middle Miocene age. MACNEIL (1973: 117) has, however, interpreted the Unga Conglomerate fauna to be slightly older.

Although many of the taxa reported here from the Unga Conglomerate Member of the Bear Lake Formation are rather wide ranging in water depth, it is clear that deposition took place under conditions ranging from subaerial to water depths no greater than about 90 m (upper part of the outer neritic zone). Much of the unit was probably depos-

ited in the inner neritic and shallow subtidal part of the inner neritic zone. Fossil wood and upright tree stumps in the Unga Conglomerate of Unga Island (BURK, 1965; EAKINS, 1970) indicate subaerial conditions. A number of small collections of mollusks from the Alaska Peninsula north of Unga Island, however, show the latter area to have been one of marine clastic deposition. The very heavy shell of *Mytilus gratacap*i suggests adaptation to high energy nearshore environments on exposed coastlines with heavy wave surge and surf (ALLISON & ADDICOTT, 1976). The heavy shelled mactrid genus *Pseudocardium* also suggests a nearshore high-energy environment and probably indicates shallow water.

The Unga Conglomerate Member was probably deposited in water of the warm temperate province [no cooler than 10° C surface temperature (HALL, 1964), substantially warmer than that of the present Gulf of Alaska]. The available small molluscan collections suggest that water temperatures were similar during deposition of the Unga Conglomerate Member and during the deposition of the remainder of the overlying Bear Lake Formation.

The very poorly known molluscan fauna of the Unga Conglomerate Member appears to contain faunal elements with both western North American and Asiatic affinities. Of the 17 taxa analyzed here, six (35%) seem to be of Asian affinities, and 4 (24%) seem related to western North American stocks. The remaining 7 taxa (41%) are either locally endemic, or endemic to the higher latitude perimeter of the North Pacific.

Bear Lake Formation, unnamed upper member:

The type locality of the Bear Lake Formation is in the mountains above and eastward from Bear Lake, just east of Port Moller. These marine clastic sedimentary rocks have been mapped by BURK (1965) on the Alaska Peninsula between Cold Bay on the west and Black Peak near Chignik Bay on the east. Bear Lake Formation beds above the Unga Conglomerate Member have not been given a member name. The overlying yellow, brown, or gray lithic subgraywackes, lithic arenites, and shales differ sharply from the volcanic detritus of the basal conglomerate. The Bear Lake Formation is at least 1525 m thick in the vicinity of Port Moller, and may be twice this thick (BURK, 1965). It is unconformably overlain by volcanic breccias, or by marine sandstone and conglomerate which I refer to the Tachilni Formation. In the Black Peak area, beds mapped as Bear Lake Formation by BURK (1965) are now known to contain a major angular unconformity. This feature separates an overlying cool-water molluscan fauna, which I consider correlative of the Tachilni Formation, from an

underlying warmer-water molluscan fauna typical of the Bear Lake Formation proper.

The Bear Lake Formation is richly fossiliferous locally. The upper part of the formation contains oysters, clams, and sand dollars which may form shell banks in which fossils constitute as much as a third of the rock volume (BURK, 1965). Nevertheless only meager collections are presently available for study. A megainvertebrate fauna of about 40 species is known from the Bear Lake Formation above the Unga Conglomerate and below the unconformably overlying strata. There is little doubt that careful collection of the Bear Lake Formation could materially enlarge the faunal list.

MACNEIL (*in* BURK, 1965) and ALLISON & ADDICOTT (1976) have considered the type Bear Lake Formation to be of provincial late Miocene age. My analysis of the molluscan fauna of the upper unnamed member of the Bear Lake Formation below the unconformity shows it to belong to the Wishkahan Stage of ADDICOTT (1976). The Wishkahan Stage is late middle to late Miocene in the sense of BERGGREN & VAN COUVERING (1974). Species which occur in the Bear Lake Formation that are not known in strata older than those of the Wishkahan Stage include *Acila* cf. *A. empirensis* Howe, *Chione* cf. *C. securis* (Shumard), *Clinocardium hannibali* Keen, *Clinocardium* sp. aff. *C. nuttalli* (Conrad), *Clinocardium* cf. *C. pristinum* Keen, *Siliqua* sp. (generic range in Pacific Northwest only), and *Tellina aragonia* Dall. In addition, *Clinocardium hannibali* Keen, *Clinocardium pristinum* Keen, and *Tellina aragonia* Dall are not known from strata younger than those of the Wishkahan Stage.

The molluscan assemblages from the Bear Lake formation are clearly indicative of deposition in the neritic zone; many of the collections are indicative of the inner neritic zone. Some assemblages bearing *Mytilus gratacap*i and *Macrocallista* n. sp. suggest very shallow subtidal deposition.

Bear Lake faunal assemblages whose stratigraphic position is not in doubt give clear indications of water temperatures warmer than at present in the Gulf of Alaska. Although the majority of genera found in the unit still occur at the latitude of the Alaska Peninsula, at least 6 are extralimital thermophiles. These genera are: *Anadara*, *Macrocallista*, *Musashia*, *Chione*, *Septifer*, and large *Turritella*. *Chione* and *Anadara* suggest water no cooler than warm temperate [no cooler than 10° C surface temperature (HALL, 1964)]. *Musashia* and *Septifer* suggest water no cooler than mild temperate, and large *Turritella* are found no farther north than at the southern limit of the North Pacific cool temperate water mass off Asia. *Macrocallista* is restricted to tropical waters today, but almost

certainly inhabited cooler water in the western and eastern North Pacific in the past. No frigidophilic extralimital genera are known from the Bear Lake Formation.

The molluscan fauna of the Bear Lake Formation is a mixture of both Asiatic and western North American faunal elements. Approximately 21% of the 29 taxa selected for faunal analysis appear to have Asiatic faunal affinities, and 48% seem related to western North American stocks. Thirty-one percent of the fauna is endemic to the high latitude perimeter of the North Pacific. About 10% of the taxa (included with the endemics) is composed of precursors of species that later achieved circumboreal distributions.

Tachilni Formation:

WALDRON (1961) applied the name "Tachilni Formation" to fossiliferous sandstone, conglomerate, and black shale that crop out along the Pacific coast of the Alaska Peninsula between Thinpoint Cove and Cape Tachilni, near the entrance to Morzhovoi Bay. The Tachilni Formation contains much volcanogenic material in which fossil mollusks occur. To the east, the formation is unconformably overlain by the Morzhovoi Volcanics, but to the west the contact between the two units is gradational. On a regional basis, the Tachilni unconformably overlies the Bear Lake Formation. The thickness is unknown, but at the Cape Tachilni type locality, more than 61 m of richly fossiliferous, poorly consolidated sandstone crops out. Fossiliferous marine sedimentary rocks in the Black Peak-Milky River area of the Alaska Peninsula unconformably overlie the fossiliferous late middle to late Miocene Bear Lake Formation. In the writer's view, these strata are coeval with the Tachilni Formation, although BURK (1965) mapped them as part of his Bear Lake unit.

The megainvertebrate fauna of the Tachilni Formation is poorly known. MACNEIL (1970) described two new mollusks, and WAGNER (1974) described three new echinoids from these beds. I have recognized 19 taxa in Tachilni Formation fossil collections, although the fauna is doubtless larger. Seven species are only known from the Alaska Peninsula. Among the remaining taxa, known occurrences suggest that the Tachilni Formation is no older than the Jacalitos Formation and no younger than the Etchegoin Formation, both of California. *Polinices galianoi* Dall is not known in beds younger than the Etchegoin Formation of the San Joaquin Basin and the basal Merced Formation of central California. *Crenomytilus coalingensis* (Arnold) is known from beds as old as the Jacalitos and Castaic Formations of California and as young as the San Joaquin Clay of the Kettleman Hills, California. *Mya elegans* (Eichwald)

suggests that the Tachilni Formation is no older than the Jacalitos Formation of California because MACNEIL (1965, p. G-23, G-30) has interpreted it to be a descendant of the provincial late Miocene Neroly Formation species, *Mya dickersoni* Clark. *Remondella waldroni* Wagner occurs with *Echinarachnius* cf. *E. ungaensis* Wagner and seems to be closely related to the only other known species of *Remondella*, *R. gabbi* (Remond) from the provincial late Miocene of California (Cierbo through uppermost Neroly Formations of Mt. Diablo area). WAGNER (1974) notes that *R. waldroni* is more highly evolved, and therefore presumably younger, than *R. gabbi*.

Although MACNEIL *et al.* (1961), MACNEIL (1970), and WAGNER (1974), have referred the Tachilni Formation to the provincial early Pliocene, the formation is here regarded as late Miocene. The Jacalitos to Etchegoin interval is probably best referred to the upper Mohnian to lower Delmontian benthic foraminifer Stages, approximately correlated with the Graysian molluscan Stage of the Pacific Northwest (ADDICOTT, 1976: 98). Because the lower part of the San Joaquin Formation, which overlies the Etchegoin Formation of California, has been radiometrically dated at 4.3 m.y. (REPENNING, 1976: 310), it is probable that the Etchegoin Formation is best referred to the latest Miocene. ADDICOTT (1976: 96 and 110) also provisionally places the Graysian Stage in the latest Miocene. For these reasons, the Tachilni Formation is here regarded as the latest Miocene, although the Miocene-Pliocene boundary may fall within it.

The Tachilni fauna appears to represent the shallow subtidal part of the inner neritic environment. Taxa whose modern analogs are restricted to shallow water include: *Kewia*, *Spisula*, *Crenomytilus*, *Macoma* cf. *M. nasuta* (Conrad), *Siliqua*, *Protothaca*, and *Mya elegans* (Eichwald). In particular, *Mya elegans* is restricted to the shallow subtidal part of the inner neritic zone.

The mollusks of the Tachilni Formation indicate cool temperate water conditions similar to the present Gulf of Alaska. Many genera are wide ranging thermally, but *Beringius*, *Spisula voyi* (Gabb) and *Mya elegans* are northern cool-water taxa. CHAMBERLAIN & STEARNS (1963) considered *Spisula voyi* to be conspecific with *S. polynyma* (Stimpson) and report that this pelecypod is thermally limited by water warmer than about 13° C mean annual temperature. No uniquely warm-water taxa are known from the Tachilni Formation.

The small sample of the Tachilni molluscan fauna suggests that about 21% of the species are related to taxa from the west coast of North America, and that about 63% are endemic to the higher latitude perimeter of the North Pacific. About 16% of the taxa are related to Asian species,

and about 26% of the fauna (included with endemics) have affinities with North Atlantic stocks which probably descended from Pacific progenitors, possibly the Tachilni taxa themselves.

Tugidak Formation:

The Tugidak Formation is a 1500 meter-thick sequence of interbedded sandstone, siltstone, and conglomeratic sandy mudstone which crops out along the coastal bluffs and intertidal reefs of Tugidak and Chirikof islands, Alaska (MOORE, 1969). These strata contain randomly distributed pebbles and cobbles of glacial-marine origin. The base of the formation is not exposed. Unnamed marine Pleistocene beds conformably overlie the Tugidak Formation on Chirikof Island (MOORE, 1969). MACNEIL (*in* MOORE, 1969), ADDICOTT (*in* MOORE, 1969) and PLAFKER (1971) have all considered the Tugidak Formation to be Pliocene. About 20 fossil collections have been examined by the writer. They show the fauna to be diverse (more than 80 species) and largely composed of living, cold-water, North Pacific and Arctic taxa.

No satisfactory biostratigraphic standard yet exists for western North American late Neogene offshore molluscan faunas, which makes interpretation of the precise age and correlation of the Tugidak fauna difficult. Accordingly, the age of the Tugidak fauna is best determined with reference to the late Pliocene and Pleistocene transgressions of Beringia (HOPKINS, 1967, 1973; HOPKINS *et al.*, 1974). No paleomagnetic geochronologic data are presently available for the Tugidak Formation.

The few extinct species in the Tugidak fauna indicate the best comparison to be with faunas of the late Pliocene Beringian and early Pleistocene Anvilian transgressions. The following Tugidak taxa have their first known appearance in strata of Beringian age: *Astarte elliptica* (Brown), *Astarte hemicymata* Dall, *Astarte montagui* (Dillwyn), *Astarte* cf. *A. nortonensis* MacNeil, *Astarte rolandi* Bernardi, *Buccinum* cf. *B. glaciale* Linnaeus, *Colus* cf. *C. spitsbergensis* (Reeve), *Epitonium greenlandicum* (Perry), *Epitonium greenlandicum smithi* MacNeil, *Plicifusus* cf. *P. brunneus* (Dall), *Polinices pallidus* (Broderip & SOWERBY), *Tachyrhynchus erosus* (Couthouy), and *Voluropsius* aff. *V. stefanssoni* Dall.

Although there is good evidence that the Tugidak fauna is no older than the Beringian transgression of late Pliocene age, the upper age limit is more difficult to establish. The presence of the very distinctive *Astarte hemicymata* in the Tugidak fauna is clear evidence of a Beringian to Anvilian late Pliocene to early Pleistocene age. *Astarte* cf. *A. nortonensis* indicates a Beringian to Einahnuhtan age.

Comparison of the molluscan fauna to the Bering Sea transgressions standard does not, however, permit recognition of the Beringian or Anvilian intervals by themselves. Therefore, it is not clear whether the Tugidak Formation is totally of late Pliocene age, totally of early Pleistocene age, or whether it contains the Pliocene-Pleistocene boundary. Fossil pectinids suggest that the upper part of the Tugidak Formation correlates with the lower part of the Yakataga Formation on Middleton Island (MACNEIL & PLAFKER *in* MOORE, 1969) and the Middleton Island section is of demonstrable Pleistocene age (PLAFKER & ADDICOTT, 1976; Plafker, oral communication, November, 1975). Available data therefore suggest that the Tugidak Formation is of late Pliocene and Pleistocene age.

Analysis of depth ranges of taxa from 20 fossil localities representing 18 different stratigraphic levels in the Tugidak Formation suggests that deposition took place in the upper part of the outer neritic zone. Eleven assemblages indicate maximum depths no greater than 145 m, and one suggests water no deeper than 111 m. Three assemblages suggest water depths no shallower than about 119 m and 5 others indicate water no shallower than about 37 m. All the assemblages studied are compatible with neritic water depths between 91 and 145 m.

Tugidak Mollusca clearly represent cold-water conditions, colder than the present Gulf of Alaska. It seems likely that the Bering Strait was open and that there were marine connections through the Arctic to the Atlantic. Species of Atlantic origin (DURHAM & MACNEIL, 1967) include *Astarte elliptica* (Brown), *Astarte montagui* (Dillwyn) [= *A. fabula* Reeve], *Hiattella arctica* (may have reached the Pacific in the tropics rather than through the Arctic, however), and *Moelleria costulata* (Möller). OCKELMANN (1954) has suggested that *Yoldia myalis* (Couthouy) also originated in the Atlantic Ocean. Several circumboreal species in the Tugidak Formation suggest that the water temperature was cooler than that at Tugidak today. These species, which do not now range as far south as Tugidak Island, include *Axinopsida* cf. *A. orbiculata* (Sars), *Nuculana pernula* (Möller), *Yoldia hyperborea*? Torrell, *Boreotrophon clathratus* (Linnaeus), *Boreotrophon truncatus* (Strøm), *Buccinum* cf. *B. angulosum nornale* Dall, *Moelleria costulata* and *Velutina undata*? Brown. Extralimital warm-water taxa are not known from the Tugidak Formation.

The Tugidak fauna is of North Pacific origin with approximately 83% of the fauna endemic to the high latitude perimeter of the North Pacific Ocean and the Bering Sea. Forty-six percent of the fauna (included with the endemics) have circumboreal distributions, and about 10% of the fauna seems to have western North American affinities.

Only about 5% of the taxa (some pectinids) suggest primary Asiatic relationships, and one species (1% of those analyzed) is cosmopolitan.

NORTHEASTERN GULF OF ALASKA STRATIGRAPHIC UNITS

The Poul Creek Formation:

The Poul Creek Formation was named by TALIAFERRO (1932) from exposures of marine sedimentary rocks which crop out along Poul Creek in the Robinson Mountains of the Yakataga District, Alaska. The formation is composed of reddish-brown-weathering massive concretionary siltstone, sandy mudstone, and fine- to medium-grained sandstone. Glauconitic sandstone is locally abundant. The upper part contains a massive non-resistant siltstone which forms a prominent topographic swale along the front of the Robinson Mountains eastward from Yakataga Reef and a prominent covered interval at the reef itself. The 1859 meter-thick formation (MILLER, 1957) is thought to overlie the Paleogene Kulthieth Formation conformably, and is conformably overlain by the Yakataga Formation in the vicinity of Cape Yakataga. The most continuous section is exposed in a south-facing cliff at the head of Yakataga Glacier in the Robinson Mountains. MILLER (1961: 242) notes that the contact with the overlying Yakataga Formation is gradational through a 15 to 61 meter interval in most places in the Yakataga District.

The contact between the Poul Creek and overlying Yakataga Formation has been variously placed by different authors. Field examination of the contact in several sections of the Robinson Mountains by C. Arie and the writer confirms MILLER's (1961) view that the contact is gradational. In the gradational interval, glauconitic sandstone and rusty-weathering siltstone of typical Poul Creek lithology alternate with typical Yakataga Formation lithology of gray-weathering sandstone containing scattered pebbles. This gradational interval generally coincides with a change in the molluscan fauna. The formational contact is best defined within the gradational interval at the most prominent break between pebble-bearing sandstones above, and rusty-weathering glauconitic siltstones or sandstones below (C. Arie, pers. commun., 1974). Use of these criteria at Yakataga Reef places the boundary above KANNO's (1971) contact, and below KANNO's (1971) interpretation of MILLER's (1957) boundary; it is therefore here considered to be at a point about 41 meters above the prominent covered interval (C. Arie, personal communication, 1974). PLAFKER & ADDICOTT (1976: 5) advocate similar criteria for the formational boundary.

The Poul Creek contains a fairly large molluscan fauna. Using the upper formational boundary advocated here, I have compiled a faunal list of 87 megainvertebrate taxa from University of Alaska collections and published reports [CLARK (1932), DURHAM (1937), PARKER (1949), MILLER (1961), MACNEIL (1961, 1965, 1967), ADEGOKE (1967), MACNEIL in MILLER (1971), KANNO (1971), ADDICOTT *et al.* (1971), KANNO (1973), and ADDICOTT (1976)].

Analysis of the molluscan assemblages and species ranges shows that the uppermost strata belong to the Pillarian Stage (ADDICOTT, 1976: 101-102). Species not known to range into strata younger than the Pillarian Stage include: *Acila gettysburgensis* (Reagan), *Pitar arnoldi* (Weaver), *Solemya dalli* Clark, *Vertipecten fucanus* (Dall), *Ancistrolepis rearensis* (Clark), *Epitonium clallamense* Durham, and *Priscofusus stewarti* (Tegland). *Anadara* aff. *A. osmonti* (Dall) and *Vertipecten fucanus* (Dall), which occur in the upper Poul Creek, are not known to occur in beds older than the Pillarian Stage.

The oldest dated beds of the Poul Creek belong to the *Echinophoria dalli* Zone (ARMENTROUT, 1975), but a refined age for the Kulthieth-Poul Creek boundary is not yet available. It should be noted that many molluscan taxa reported by KANNO (1971) are from stratigraphically lower beds exposed in the Sullivan Anticline, but these beds are not in the lowermost part of the formation which crops out at the head of Yakataga Glacier, in the Grindle Hills, and along the Kosakuts River (KANNO, 1971: 14). The following species, from the lowermost Poul Creek Formation, are not known to range into strata older than those of the *Echinophoria dalli* Zone: *Cyclocardia* aff. *C. hannibali* (Clark), *Panopea snohomishensis* Clark, *Pitar* aff. *P. dalli* (Weaver), *Solena* aff. *S. eugenensis* (Clark), *Thracia* cf. *T. condoni* Dall, *Molopophorus stephensoni* Dickerson, *Perse olympicensis* Durham, and *Perse olympicensis quimperensis* Durham. Species which occur in the lowermost Poul Creek Formation and are not known in beds younger than the *Echinophoria dalli* Zone include *Nemocardium weaveri* (Anderson & Martin), *Solen townsendensis* Clark, *Molopophorus stephensoni* Dickerson, *Perse olympicensis* Durham, and *Perse olympicensis quimperensis* Durham.

MILLER's (1961: 243-245) report of *Patinopecten* (*Lituyapecten*) from the uppermost part of the Poul Creek Formation can be disregarded because these strata are now included in the basal part of the overlying Yakataga Formation. ADDICOTT (1972: 12) notes that *Patinopecten* has its earliest occurrence in the "Temblor Stage" (=Newportian Stage) of California. The appearance of *Patinopecten* (*Lituyapecten*) in the basal beds of the Yakataga Formation is taken here to mark the beginning of Newportian time.

Following BERGGREN & VAN COUVERING's (1974) chronology, the Poul Creek Formation ranges in age from the late Eocene (upper Refugian benthic foraminifer Stage) to the early Miocene (lower Sautesian benthic foraminifer Stage).

Evaluation of Poul Creek molluscan assemblages indicates that deposition took place in the lower inner neritic and outer neritic depth zones. Among 10 assemblages which contain genera suggestive of minimal water depth, 2 indicate water no shallower than about 21 meters, 6 no shallower than 37 meters, and 2 no shallower than 50 meters. Four assemblages indicate water depths no greater than about 111 meters, 3 no deeper than 143 meters, 1 no deeper than 165 meters, and 3 no deeper than 186 meters. RAU (1963) infers water depths between 61 and 244 meters (outer neritic to uppermost bathyal) from a benthic foraminiferal assemblage near the top of the formation.

The Poul Creek fauna is indicative of warm-water similar to the present North Pacific warm temperate belt (HALL, 1964). The oldest fossil assemblages include the genera *Nemocardium*, *Solen*, *Turritella*, *Cylichna*, *Exilia*, *Parvoicardium*, *Pitar* and *Spisula*, as well as the extinct gastropods *Molopophorus* and *Perse*; these taxa appear to indicate a warm temperate marine climate.

Several genera in the middle to upper parts of the formation indicate temperatures no cooler than the warm temperate zone; these are: *Crassatella*, *Macrocallista*, *Papyridea*, and *Eosiphonalia*. Genera which suggest temperatures no warmer than the warm temperate zone include *Clinocardium*, *Cyclocardia*, *Mya*, *Nemocardium*, *Ancistrolepis*, *Bathybembix*, *Colus*, *Natica* (*Cryptonatica*), and *Pteropurpura*. The youngest (Pillarian) Poul Creek strata also contain very large specimens of *Panomya arctica* (Lamarck) (C. Arie, personal communication, 1975), a species which does not range into water warmer than that of the mild temperate zone today. Some evidence suggests the beginning of cooling conditions during latest Poul Creek time; the bulk of the data, however, indicate the Poul Creek molluscan faunas to be of warm temperate character.

The Poul Creek fauna is most closely related to that of the Tertiary of the Pacific northwest coast of North America. Approximately 52% of the Poul Creek species have western North American affinities and about 18% of the fauna is related to that of Asia. Approximately 30% of the Poul Creek fauna was locally endemic, or was distributed around the high latitude North Pacific perimeter. Six percent of the fauna (included with the endemics) is composed of precursors of taxa that later achieved circumboreal distributions. Although these numbers differ somewhat from those of KANNO (1971: 17), they suggest the same relative

weighting between North American, Asian, and endemic faunal elements.

The Yakataga Formation:

The Yakataga Formation was named by TALIAFERRO (1932) for "a thick series of sandstones, dark shales, and conglomerates" which overlies the Poul Creek Formation at Yakataga Reef and in the Sullivan Anticline area of the Robinson Mountains. PLAFKER & ADDICOTT (1976: 6) have designated the type section as an 1800 meter-thick sequence of beds between the contact of the Poul Creek Formation at the head of Poul Creek and the southern margin of Guyot Glacier north of Munday Peak. The Yakataga Formation extends over a broad area of the northeastern Gulf of Alaska, from the Suckling Hills of the Katalla district on the west to Icy Point in the Lituya district on the east. It also crops out on Kayak, Middleton, and Wingham islands, and probably occurs over much of the adjacent continental shelf of the Gulf of Alaska (*op. cit.*, p. 4). It has a composite thickness of about 5000 m (*op. cit.*) of which the upper 1181 m are exposed on Middleton Island (PLAFKER, 1971). A major intraformational unconformity occurs within 1500 m of the base of the formation in the Yakataga-Malaspina districts (ADDICOTT & PLAFKER, 1976: 15). Till-like glaciomarine diamictite or "conglomeratic sandy mudstone" occurs in all but the basal part, and is abundant in much of the formation (*op. cit.*, p. 9). Glaciomarine dropstones occur in all lithologies and are primary components of the diamictites. Glacial striae are observed on scattered clasts (*op. cit.*, p. 9b-10).

Although the youngest outcrops are on Middleton Island, marine seismic profiling and bottom sampling indicate that the youngest part of the formation includes unlithified Holocene deposits (PLAFKER & ADDICOTT, 1976: 6). The oldest strata assigned to the Yakataga Formation occur on Kayak Island (PLAFKER, 1974; PLAFKER & ADDICOTT, 1976) and are older than the basal Yakataga Formation beds at Yakataga Reef and in the Sullivan Anticline area.

This section of the paper deals primarily with the pre-Pleistocene faunas of the Yakataga Formation of the Katalla, Yakataga, Malaspina, Yakutat, and Lituya districts. The Pleistocene portion of the Yakataga Formation at Middleton Island is treated separately.

The oldest strata recognized in the formation occur on Kayak and Wingham islands. Although a number of molluscan taxa are reported from Kayak and Wingham islands by ADDICOTT in PLAFKER (1974), only two stratigraphically significant species, *Acila gettysburgensis* (Reagan) and *So-*

lemya dalli Clark, occur in these strata. The co-occurrence of these taxa in the "lower part of the Yakataga Formation" (PLAFKER, 1974), south of the Kayak Fault on eastern Kayak Island, indicates a Juanian to Pillarian age, that is, latest Oligocene to early Miocene in the sense of BERGGREN & VAN COUVERING (1974). PLAFKER (1974) reports a sparse foraminiferal assemblage of possible Zemorrian, and therefore probable, Juanian age.

Slightly younger strata on Kayak Island, referred to the "upper part of the Yakataga Formation" (PLAFKER, 1974) also contains *Acila gettysburgensis*. The co-occurrence of this species, which is not known to range into strata younger than Pillarian age (ADDICOTT, 1976b) with foraminiferal assemblages of Saucian or Relizian age (PLAFKER, 1974) suggests that these strata belong to the Pillarian Stage of the early Miocene. Recognition of Juanian (?) and Pillarian strata in the lower Yakataga Formation indicates that the upper Poul Creek Formation of the Yakataga area and the lower Yakataga Formation of Kayak Island are coeval.

Strata near the base of the Yakataga Formation at Yakataga Reef are here considered to belong to the late early to early middle Miocene Newportian Stage. The Newportian age is based on the presence of *Macoma arctata* (Conrad) (KANNO, 1971, loc. 80605), which is not known to occur in strata younger than those of Newportian age, and the genus *Patinopecten* which is not known to occur in strata older than those of the Newportian Stage (ADDICOTT, 1974: 183; 1976: 98). The lowest known stratigraphic occurrence of *Patinopecten* at the reef seems to be that of KANNO (1971: 53, and USGS loc. M271, probably equal to Kanno's loc. 80903). This locality is approximately 10 meters above the Poul Creek-Yakataga contact, as used here (see discussion under Poul Creek Formation) or about 51 m stratigraphically above the prominent covered shale of the upper Poul Creek Formation at the reef (measured section of C. Arie, personal communication, August, 1976). PLAFKER & ADDICOTT (1976) also list *Molopophorus matthewi* Etherington from the lower Yakataga Formation in the Yakataga district; although the exact stratigraphic position is not reported, this species is considered to be restricted to the Newportian Stage.

Unpublished research by C. Arie (personal communication, June, 1977) suggests that the Newportian-Wishkahan boundary is located approximately 30 m above the base of the Yakataga Formation, and that Newportian strata therefore constitute a very thin stratigraphic interval in the Yakataga District. This conclusion is based upon the first appearance of *Siliqua* and *Yoldia* (*Cnesterium*) which are thought to be indicative of strata no older than the Wishkahan Stage in the northeastern Pacific. Other modern taxa which first appear in this stratigraphic posi-

tion include *Mya truncata* Linnaeus, *Solamen* cf. *S. columbianum* (Dall), *Miyagipecten* sp., *Yabepecten* sp., *Laqueus californianus* (Koch), and *Bittium* cf. *B. frankeli* Faustman (personal communications, C. Arie and S. McCoy, Jan., 1978).

Deposits of Wishkahan, Graysian, Moclipsian, and younger are clearly present in the Yakataga Formation, but the boundaries between these stages, as well as those of the European series-epochs, are presently extremely difficult to place. This stems from lack of published faunal lists for specific fossil localities of known stratigraphic position in the part of the formation stratigraphically above Yakataga Reef, as well as from the increase of endemic and living species in these younger strata. PLAFKER & ADDICOTT (1976: 22) observe that correlation is also hindered by the tendency of late Cenozoic cold-water mollusks to be unusually long-ranging.

WAGNER (1974) notes the presence of *Scutellaster oregonensis* (Clark) in the Yakataga Formation of the La Perouse Glacier and Topsy Creek areas of the Lituya District. This species is restricted to strata of Wishkahan age in the Pacific Northwest. MASUDA & ADDICOTT (1970) questionably report *Yabepecten condoni* (Hertlein) [= *Miyagipecten alaskensis* MacNeil] from a nunatak north of the east end of the Pinnacle Hills in the Malaspina district; this species appears to be restricted to deposits of Graysian age (ADDICOTT, 1976). MACNEIL (1961) reported *Patinopecten* (*Lituyapecten*) cf. *P. (L.) dilleri* (Dall) from the coast south of Lituya Bay; *P. (L.) dilleri* s. s. is restricted to deposits of Moclipsian age (ADDICOTT, 1976). Although the geographic occurrence is unknown, the appearance of a species of Atlantic origin, *Astarte* aff. *A. elliptica* (Brown) [= *A. alaskensis* Dall], about 2438 m above the base of the Yakataga (MACNEIL in MILLER, 1971; MACNEIL, 1965: 6-8) is indicative of a Beringian or younger age. Many other molluscan taxa indicative of Beringian and younger ages occur in the upper Yakataga Formation of the mainland. *Chlamys chaixensis* MacNeil and *Chlamys lioica* (Dall) co-occur in the highest Yakataga strata in the Chaix Hills of the Malaspina District; these beds are no older than the Beringian transgression, and are probably Anvilian (early Pleistocene) in age (PLAFKER & ADDICOTT, 1976). These strata may be younger than the *Chlamys* (*Leochlamys*) *tugidakensis* range zone of Tugidak and Middleton Islands.

In summary, the oldest strata of the Yakataga Formation occur on Kayak Island; they are at least as old as the Pillarian Stage, and could be as old as the Juanian Stage. The youngest Yakataga strata in the Yakataga to Lituya districts are probably coeval with the Middleton Island Anvilian beds and could be in part younger than the *Chlamys* (*Leochlamys*) *tugidakensis* Range Zone. The Yakataga

Formation therefore appears to range from late Oligocene (?) or early Miocene (Juanian? to Pillarian) to early Pleistocene (Anvilian).

The oldest Yakataga strata, at Kayak and Wingham islands, were deposited in upper bathyal water depths. The lower Yakataga of the Yakataga District seems to have been deposited in lower inner neritic to outer neritic water depths. Younger parts of the formation in the Malaspina to Lituya districts to the southeast may be inner neritic. The youngest beds of the formation at Kulthieth Mountain and Pinnacle Pass appear to be intertidal to shallow sublittoral deposits. It therefore appears that water depth became generally shallower upsection. Although not as well documented, there also seems to be a trend from deeper water offshore to shallower water onshore in the north and easterly directions.

Yakataga molluscan faunas clearly indicate cooler water than that of the underlying Poul Creek Formation. Mollusks from the lowermost part of the Yakataga Formation on Kayak Island (Juanian? Stage) appear to indicate mild temperate conditions, probably slightly cooler than those during deposition of contemporary strata of the Yakataga District. This apparent discrepancy probably reflects the deeper, and therefore cooler, environment of deposition at Kayak Island. The "upper part of the Yakataga Formation" (PLAFKER, 1974) at Kayak Island (Pillarian Stage) and Pillarian strata of the Poul Creek Formation in the Yakataga District also seem to have been deposited in mild temperate water. Yakataga molluscan assemblages reported by KANNO (1971) from Yakataga Reef (Newportian and probably Wishkahan) suggest slightly cooler temperatures, probably like those near the mild temperate-cool temperate boundary. A number of small collections from the lower Yakataga of the Sullivan Anticline and Yakataga District (KANNO, 1971) also suggest mild temperate to cool temperate conditions.

Stratigraphically higher beds in the Karr Hills and the Samovar Hills (KANNO, 1971) probably were deposited in cool temperate water; these strata appear to be no older than Graysian (late Miocene). Strata which appear to be no older than the late Pliocene Beringian transgression also contain molluscan assemblages indicative of water no warmer than the cool temperate climatic zone.

Yakataga molluscan assemblages therefore demonstrate that climatic deterioration continued during Miocene and Pliocene time. By early Pleistocene (Anvilian) time, the molluscan data indicate the presence of cold-water conditions (see section on Middleton Island Yakataga Formation).

All workers who have considered the paleoclimatology (e.g. BANDY *et al.*, 1969; KANNO, 1971; PLAFKER & ADDI-

COTT, 1976) agree that there was a temperature drop during late Poul Creek to earliest Yakataga time. My interpretation of the Yakataga molluscan and planktonic foraminifer data is, however, in disagreement with the views of earlier workers in that I believe mild temperate and cool temperate rather than cold (Arctic) conditions existed throughout much of Yakataga time.

KANNO (1971:24) suggests that the entire Yakataga Formation was deposited in "Arctic" water temperatures comparable to those north of the present southern limit of winter sea ice. PLAFKER & ADDICOTT (1976) refer to a sharp decline in temperature across the formational contact from "temperate" to "cold" conditions, but do not specify how cold the Yakataga may have been.

BANDY *et al.* (1969) offer an interpretation similar to KANNO (1971) in suggesting a 10° to 15° C temperature drop across the formational boundary. This interpretation is based on an influx of left-coiling *Turborotalia pachyderma* (Ehrenberg) near the base of the Yakataga Formation in the Yakataga District. BANDY *et al.* (1969) indicate that this planktonic foraminifer is similar to those now restricted to polar waters with summer surface temperatures of about 2° C.

HERMAN (*in* ALLISON, 1973) points out, however, that the range of sinistral *T. pachyderma* is between -1° C and 5° C, but that it is occasionally found in waters up to 15° C. BANDY (1968b) notes the common occurrence of predominantly sinistral *T. pachyderma* in waters with 2° to 8° C summer temperatures, and BANDY (1968a) also points out that the southern boundary of the common sinistral *T. pachyderma* fauna appears to be about 45° north latitude in the eastern Pacific off Oregon, and perhaps near 50° north latitude in the central and western Pacific. These latitudes embrace the cold or Arctic zone, the cool temperate zone, and parts of the mild temperate belt. On the basis of my study of the Mollusca and data (BANDY, 1968a, 1968b; HERMAN *in* ALLISON, 1973) on *Turborotalia pachyderma* it does not appear to me that the cold water (Arctic) paleotemperature interpretations for the bulk of the Yakataga Formation are defensible. Both the molluscan and planktonic foraminifer data are compatible with mild temperate to cool temperate conditions suggested here for the pre-Beringian portions of the formation. The Beringian and Anvilian parts of the formation, however, do appear to have been deposited in cold (Arctic) waters.

Although the Yakataga molluscan fauna is incompletely known, some general paleozoogeographic trends are indicated. About 41% of the taxa of the lower Yakataga Formation at Kayak and Wingham Islands is composed of species with Asiatic affinities. Asiatic paleozoogeographic affinities are less apparent in the younger (Newportian and

Wishkahan?) beds at Yakataga Reef (about 12%) and in strata younger than those of Yakataga Reef (Graysian? and younger) (about 10%). Faunal affinities with the west coast of North America increase slightly from about 14% at Kayak and Wingham islands to about 28% at Yakataga Reef and about 26% for younger strata.

The fauna of the Yakataga Formation is marked by the large number of taxa which are endemic to the high latitude perimeter of the North Pacific or to the local outcrop area. Endemic species constitute about 45% of the fauna at Kayak and Wingham islands and increase to about 58% at Yakataga Reef. Strata younger than those of Yakataga Reef contain faunas with about 62% endemic taxa.

Of interest is the number of precursors to present circumboreal taxa in the Yakataga Formation. In fact, the Kayak and Wingham islands Yakataga faunas include two taxa (about 9% of the fauna; included with the endemics) that probably are ancestral to modern circumboreal species. Five of the endemic taxa (12% of the fauna) from Yakataga Reef also appear to be precursors of present circumboreal taxa. About 26% (included with the endemics) of the Yakataga fauna from strata younger than those at Yakataga Reef show circumboreal paleogeographic affinities.

One cosmopolitan species, *Hiatella arctica*, (2% of the fauna) occurs at Yakataga Reef, and another, *Mytilus edulis*, (3% of the fauna) occurs in Yakataga strata younger than those of Yakataga Reef.

The large endemic component of the faunas (62% of the fauna in strata younger than those at Yakataga Reef) creates a major problem in correlation of these strata with coeval deposits of the west coast of the conterminous United States.

Yakataga Formation on Middleton Island:

Late Cenozoic glaciomarine strata crop out in the coastal bluffs and on the intertidal platforms of Middleton Island, which is located in the north-central Gulf of Alaska. PLAFKER (1971) assigned these strata to the uppermost Yakataga Formation and reports their thickness to be 1181 m. Marine fossils are sparsely distributed throughout the formation in conglomeratic sandy mudstone, fine-grained sandstone and in siltstone.

Although a number of investigators have variously regarded the Middleton Island Yakataga beds as Pliocene or Pleistocene (MILLER, 1953; MACNEIL, *et al.*, 1961; HOPKINS, 1967; MACNEIL, 1967; ADDICOTT, 1971), there is no convincing biostratigraphic means of recognizing the Pliocene-Pleistocene boundary in the Gulf of Alaska region. PLAFKER & ADDICOTT (1976) and Plafker (personal communication, Nov., 1975) report that recent geomagnetic stratigraphy studies show the Middleton Island Yaka-

taga Formation to belong to the Matuyama reversed polarity epoch (no younger than 0.7 million years b.p.). The very lowest strata exposed at Middleton Island possess normal geomagnetic polarity, possibly indicating the Olduvai event of earliest Pleistocene time (-1.6 to 1.8 m.y.; BERGGREN & VAN COUVERING, 1974: 140). The Middleton Island section is therefore here considered to be of Anvilian (early Pleistocene) age with the Pliocene-Pleistocene boundary near, but below, its base.

About 65 fossil collections from the Middleton Island Yakataga Formation have been examined. Many of these are small, but they range throughout the stratigraphic section. These collections show the fauna to be somewhat less diverse (in excess of 70 species) than that of the Tugidak Formation, and on the whole not as well preserved. The molluscan fauna is largely composed of living cold-water North Pacific and boreal species, and contains about 35 taxa in common with the Tugidak Formation. This difference in faunal composition probably owes in part to difference in geological age as suggested by the distinct *Chlamys* and *Astarte* species; a more fundamental cause, however, probably is the somewhat different ecologic setting at Middleton.

The fossil Mollusca clearly indicate that the Middleton Island Yakataga Formation is younger than the Tachilni Formation of the Alaska Peninsula, and that it is no older than the Beringian transgression. The following species, which occur, or are questionably reported, in the Middleton Island section, make their earliest appearance in strata of Beringian age: *Astarte elliptica* (Brown), *Astarte montagui* (Dillwyn), *Astarte rollandi* Bernardi, *Buccinum glaciale* Linnaeus, *Buccinum glaciale parallelum* Dall, *Buccinum physematum* Dall, *Buccinum plectrum* Stimpson, *Epitonium greenlandicum* (Perry), *Plicifusus kroyeri* (Möller), *Polinices pallidus* (Broderip & Sowerby), and *Tachyrhynchus erosus* (Couthouy).

Although the lower age limit for this fauna is readily established with the fossil Mollusca, recognition of the upper age limit depends upon the presence of extinct species. Monographic treatment of the pectinids by MACNEIL (1967) and the neptuneids by NELSON (1974) make possible the recognition of the only extinct taxa so far known in the Middleton Island Yakataga Formation. The following extinct species have been recognized: *Chlamys hanaishiensis amchitkana* MacNeil, *Chlamys islandica kanagae* MacNeil, *Chlamys* cf. *C. picoensis chinkopensis* Masuda & Sawada, *Chlamys pseudoislandica plafkeri* MacNeil, *Chlamys coatsi middletonensis* MacNeil, *Chlamys tugidakensis* MacNeil, and *Neptunea lyrata altispira* Gabb.

These taxa indicate an age no younger than the middle Pleistocene Kotzebuan or Einahnuhtan transgressions (HOPKINS, 1973), but the paleomagnetic evidence of an age no younger than the early Pleistocene part of the Matu-

yama reversed polarity epoch (Anvilian transgression) is thought to be the most reliable criterion for dating this sequence.

Although early collections studied by MACNEIL (1967) showed *Chlamys tugidakensis* to range only through the lower 762 m of the Middleton Island section, it is now recorded to approximately 1109 m above the base, and therefore almost throughout the entire stratigraphic succession, a situation also found at Tugidak. In short, both the Middleton Island Yakataga Formation and the Tugidak Formation belong almost entirely to the range zone of *Chlamys tugidakensis* and this species appears to continue across the Pliocene-Pleistocene boundary. Strata of the upper Yakataga Formation in the Chaix Hills of the Lituya District also belong to the range zone of *Chlamys tugidakensis*.

Chlamys cf. *C. picoensis chinkopensis* occurs from near the base of the Middleton Island section to about 732 m above the base. This species also is known from a locality 97.5 m below the top of the Tugidak Formation, which suggests that the top of the Tugidak Formation and some part of the basal Middleton Island Yakataga Formation section may be coeval. The absence of species of *Astarte* in the Middleton Island section, which are restricted to the Beringian-Anvilian interval in the Bering Sea area and at Tugidak, also suggests that much of the Middleton Island section may be younger than the Tugidak Formation.

Analysis of the Middleton Island assemblages shows 8 with lower depth limits of 50 m, 3 with depth limits at 55 m, 11 with limits no deeper than 74 m, and one each limited to water no deeper than 75 m, 119 m, and 136 m. Five assemblages appear to be limited to water no deeper or no shallower than about 50 m.

Analysis of the Middleton Island molluscan assemblages also shows 7 with water no shallower than 15 or 18 m, 5 limited to water no shallower than depths between 21 and 46 m, and most significantly, 16 assemblages limited to water no shallower than 50 m. One assemblage appears to be limited to depths no shallower than 55 m, 64 m, 76 m, and 94 m.

To summarize, these data suggest that most assemblages lived between 50 and 74 m, and that locally the bottom could have been as shallow as 15 or 18 m, and as deep as 136 m at one stratigraphic level near the base of the exposed section. The bulk of the data therefore suggests depths in the lower part of the inner neritic or top of the outer neritic depth zones. The data also suggest that water depths were generally shallower at Middleton Island than at Tugidak, and this appears to have been a significant factor in determining the somewhat different faunas of the two areas.

Mollusks from the Middleton Island Yakataga Formation represent cold-water conditions, colder than exist in

the Gulf of Alaska today. Although most of the species are endemic to the North Pacific, my data show that about 35% (included with the endemics) are circumboreal taxa that range throughout the Arctic or into the North Atlantic. Eight species found in the Middleton Island strata are not presently known to live near Middleton, but are confined to areas farther west along the Aleutians or farther north in the Bering Sea. These cold-water extralimital taxa are: *Nuculana pernula* (Möller), *Yoldia* cf. *Y. arctica* (Gray), *Beringius frielei* Dall, *Buccinum tenue lyperum* Dall, *Volutopsius* cf. *V. middendorffi* (Dall), and *Volutopsius* cf. *V. simplex* Dall. Two species in the Yakataga Formation at Middleton Island have not been reported living this far north. These two southern extralimital species are *Laqueus californianus* (Koch) (known as far north as British Columbia), and *Taranis strongi* (Arnold) (known to 55° N latitude at Forrester Island, Alaska). In summary, the evidence suggests that the Gulf of Alaska was indeed colder than at present during deposition of the Middleton Island Yakataga Formation.

As in the Tugidak fauna, most of the Middleton Island Yakataga fauna is of North Pacific origin. Approximately 75% of the taxa have modern North Pacific distributions suggesting no closer relationship to Asia than to North America. Among the circumboreal species, which constitute about 35% (included with the endemics), the great majority originated in the Pacific (DURHAM & MACNEIL, 1967). *Astarte elliptica* (Brown) and *Astarte montaguui* (Dillwyn) are faunal elements of Atlantic origin which suggest that the Bering Strait was open during or prior to deposition of the Middleton Island strata. The pectinid fauna is of North Pacific origin, although it is most closely related to forms known in Japan; at most, about 5% of the fauna can be considered to show Asiatic zoogeographic affinities. Approximately 18% of the fauna suggests faunal relationships with western North America, and about 2% may be considered cosmopolitan. One species, *Chlamys islandica kanagae* MacNeil (2% of the fauna; included with the endemics) appears ancestral to a North Atlantic taxon.

SUMMARY AND CONCLUSIONS

Tables 1 and 2 summarize data on the mollusk-bearing stratigraphic units discussed; Figure 2 also shows suggested correlations among them.

Analysis of these data permit several conclusions:

1. Neogene thermal histories of the western and north-eastern Gulf of Alaska were distinctly different from each other (ADDICOTT, 1969). The western Gulf had a climatic history similar to that of the conterminous

Table 1

Summary of data for some western Gulf of Alaska mollusk-bearing stratigraphic units. Because of dubious specific and generic identifications, the number of systematic entries on the faunal lists used for analysis differs from the number of taxa actually present. The number of taxa amenable to zoogeographic analysis is given in parentheses

Western Gulf of Alaska

Formation	Thickness	Age	Water depth	Temperature	Zoogeographic affinities (Figures very approximate)	No. of systematic entries (No. taxa analyzed)
Tugidak Formation	1500m	Beringian to Anvilian transgressions	upper outer neritic	cold	Asiatic: 5% North American: 10% Endemic: 83% (Circumboreal: 46%) Cosmopolitan: 1%	98 (78)
Tachilni Formation	61m +	Graysian ("Jacalitos" to "Etchegoin")	shallow subtidal to inner neritic	cool temperate	Asiatic: 16% North American: 21% Endemic: 63% (Pre-circumboreal: 26%)	20 (19)
Upper Unnamed Member of the Bear Lake Formation	1525m to possibly 3000m(?)	Wishkahan	shallow subtidal to inner neritic	warm temperate	Asiatic: 21% North American: 48% Endemic: 31% (Pre-circumboreal: 10%)	48 (29)
Unga Conglomerate Member of the Bear Lake Formation	244m	late Newportian to early Wishkahan	subaerial to upper outer neritic	warm temperate	Asiatic: 35% North American: 24% Endemic: 41%	25 (17)
Narrow Cape Formation	700m	Newportian	shallow subtidal to outer neritic	warm temperate, perhaps near outer tropical boundary	Asiatic: 33% North American: 53% Endemic: 13% (Pre-circumboreal: 3%)	45 [Fauna includes about 80 taxa, however] (30)
Narrow Cape Formation of Sitkinak Island	210m	Juanian	outer neritic	near cool temperate-mild temperate boundary	Asiatic: 32% North American: 35% Endemic: 30% (Pre-circumboreal: 14%) Cosmopolitan: 3%	57 (37)

western United States. In contrast, Miocene temperatures of the northeastern Gulf were cooler and appear to be related to local glaciation which began about 20 million years ago (PLAFKER & ADDICOTT, 1976).

2. Sea surface temperatures in the northeast Gulf were as warm as the mild temperate zone when glaciation began; temperatures cooler than the present cool temperate conditions were not reached before late Pliocene (Beringian) time. The thermal history proposed here differs significantly from those of BANDY *et al.* (1969) and KANNO (1971) who inferred cold-water (Arctic) conditions throughout Yakataga time.

3. Asiatic faunal affinities are generally greater in the western Gulf area than in the northeastern area; both show significant declines during Miocene time.
4. North American faunal affinities are most pronounced during periods of relatively warm water conditions as represented by the faunas of the Poul Creek, Narrow Cape, and upper Bear Lake Formations. Substantially fewer taxa with North American affinities are recorded in the faunas of the Yakataga, Tachilni, and Tugidak Formations; these decreases are correlated with cooler water temperatures and increased provincialism and faunal endemism.

Table 2

Summary of data for some northeastern Gulf of Alaska mollusk-bearing stratigraphic units. Because of dubious specific and generic identifications, the number of systematic entries on the faunal lists used for analysis differs from the number of taxa actually present. The number of taxa amenable to zoogeographic analysis is given in parentheses.

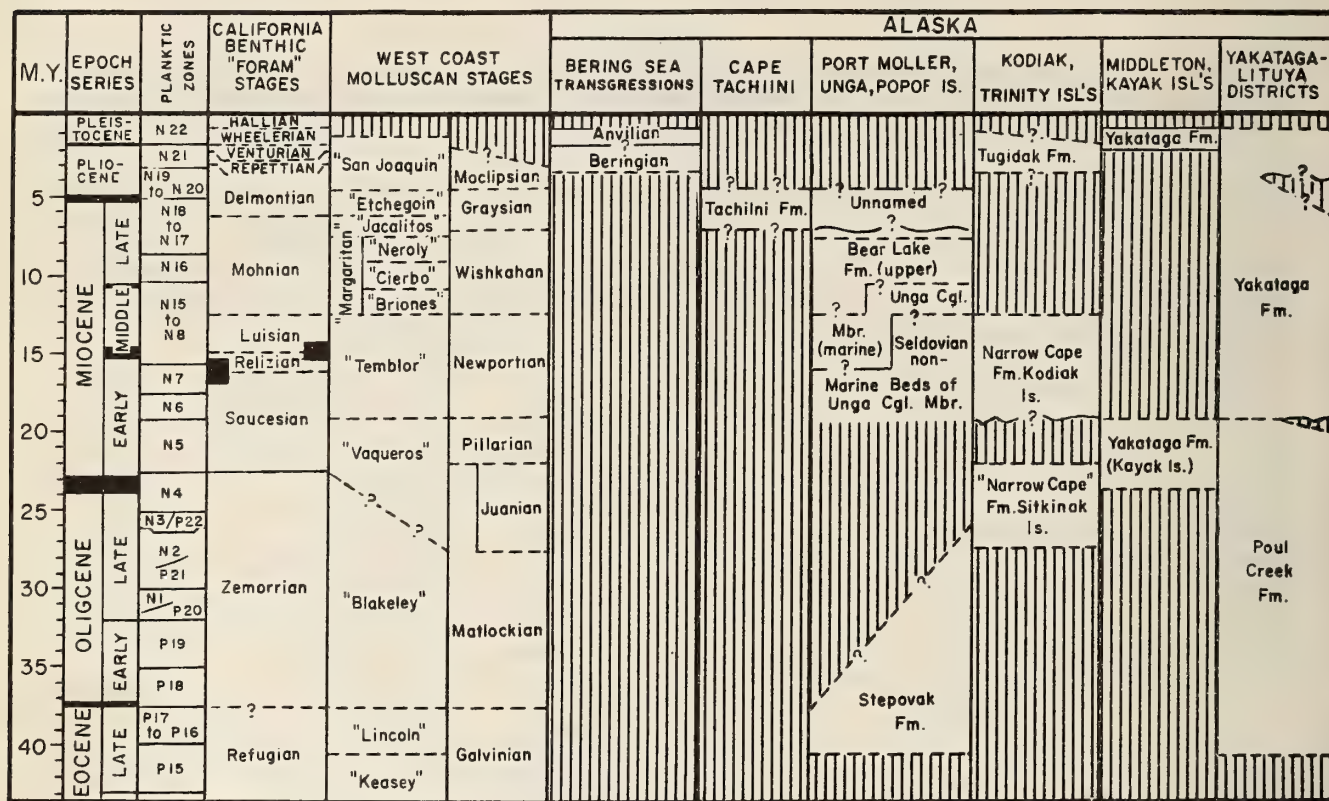
Formation	Thickness	Age	Water depth	Temperature	Zoogeographic affinities (Figures very approximate)	No. of systematic entries (No. taxa analyzed)
Yakataga Formation at Middleton Island	1181 m	Anvilian transgression	lower inner neritic to upper outer neritic; occasionally shallower	cold	Asiatic: 5% North American: 18% Endemic: 75% (Circumboreal: 35%) (Pre-circumboreal: 2%) Cosmopolitan: 2%	115 (60)
Yakataga Formation (Mainland, Kayak and Wingham Islands)	~5000 m including Middleton Is. beds	Anvilian? transgression at top (Chaix Hills)	intertidal and shallow subtidal to inner neritic in upper part	cold at top? cool temperate in upper part	Asiatic: 10% North American: 26% Endemic: 62% (Pre-circumboreal and Circumboreal: 26%) Cosmopolitan: 3%	42 (39)
		Newportian at base at Yakataga Reef	lower inner neritic to outer neritic at Yakataga Reef	near mild temperate-cool temperate boundary at Yakataga Reef	Asiatic: 12% North American: 28% Endemic: 58% (Pre-circumboreal: 12%) Cosmopolitan: 2%	48 (43) 121 (104)
		Juanian? and Pillarian at base on Kayak Island	upper bathyal at base on Kayak Is.	mild temperate at base on Kayak Island	Asiatic: 41% North American: 14% Endemic: 45% (Pre-circumboreal: 9%)	31 (22)
Poul Creek Formation	1859 m	<i>Echinophoria dalli</i> zone (upper Galvinian) to Pillarian	lower inner neritic to outer neritic	mild temperate at top ----- warm temperate	Asiatic: 18% North American: 52% Endemic: 30% (Pre-circumboreal: 6%)	107 (87)

Northeastern Gulf of Alaska

- In general, species that are locally endemic or endemic to the high latitude perimeter of the North Pacific are more abundant in the northeast Gulf of Alaska area. Faunal endemism is at a minimum during warm-water conditions.
- Some taxa appeared in the Gulf of Alaska prior to the late Pliocene (Beringian) opening of the Bering Strait, and later achieved circumboreal distributions or gave rise to taxa that did. These "pre-circumboreal" taxa are therefore a special category of North Pacific endemic species. The earliest of these taxa appear in Juanian (late Oligocene) strata of the Gulf.

They increase upsection in cool-water units, but decrease during warm-water conditions.

- Endemic (includes "pre-circumboreal" and circumboreal) taxa increase upsection in the Yakataga Formation to a maximum of 75% of the Middleton Island fauna. This group increases upsection in the western Gulf to 83% in the Tugidak Formation. These data underscore the difficulty in correlating the late Neogene and Quaternary molluscan faunas of the Gulf with conterminous western United States faunas.



Richard C. Allison, 1977

Figure 2

Tentative correlations of major late Paleogene to Pleistocene mollusk-bearing stratigraphic units of the Gulf of Alaska Region. Radiometric time-scale, epochs, planktonic zones, and California benthic foraminifer stages adapted from BERGGREN & VAN COUVERING (1974: figs. 1 and 15) and modified by reference to EVERENDEN *et al.* (1964), LIPPS (1967), TURNER (1970), BERGGREN (1972), HORNADAY (1972), LIPPS & KALISKY (1972), STAINFORTH *et al.* (1975), and HOWELL (1976). The California benthic chronology is, however, tied to the planktonic zones and radiometric time-scale by relatively few control points. Several authors (*e.g.*, INGLE, 1967; BANDY, 1972; and PIERCE, 1972) have suggested that some California benthic foraminifer stage boundaries may be time-transgressive, thereby further complicating correlations.

The West Coast molluscan stage chronologies are adapted from WEAVER *et al.* (1944), DURHAM *et al.* (1954), ADEGOKE (1969), ADDICOTT (1972), ARMENTROUT (1975), and ADDICOTT (1976). The molluscan stages are somewhat loosely tied to the benthic foraminifer stages and to the North American land-mammal ages for which some radiometric dates are available (EVERENDEN *et al.*, 1964, and SAVAGE, 1972).

The Alaskan molluscan faunas have been correlated with the West Coast molluscan chronologies and the Bering Sea transgression cycles (HOPKINS, 1967). Vertical ruling indicates either hiatus, or absence of major mollusk-bearing stratigraphic units. Thick black lines at the sides of some chronostratigraphic boundaries indicate the probable range of accuracy of the boundary position as determined by radiometric dating.

8. Analysis of the biogeographic affinities of the faunas suggests that the first exchange of North Pacific and North Atlantic taxa through the Bering Strait may have been during the late Miocene, perhaps at the beginning of Wishkahan time some 10 to 13 million

years ago (HOPKINS, 1967b: 454). The later Beringian (late Pliocene) opening of the Bering Strait permitted many North Pacific taxa to migrate into the North Atlantic (HOPKINS, *loc. cit.*) and allowed a lesser number of North Atlantic and boreal species

to reach the Bering Sea and North Pacific (DURHAM & MACNEIL, 1967).

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World-Wide Biostratigraphic Correlation Based on Turritellid Phylogeny

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(7 Text figures)

INTRODUCTION

THE FAMILY TURRITELLIDAE includes several taxa that have generally restricted dispersal ability because of their very short veliger stage and ovoviviparity in some cases (LEBOUR, 1933; MARWICK, 1971; MERRIAM, 1941; PALMER, 1958, 1961; PEILE, 1922), therefore, genetically isolated groups must have diverged widely from each other during the course of Cretaceous and Tertiary time. In natural classification, this should be reflected by numerous localized genera and subgenera. According to MARWICK (1957), more than a thousand fossil and living species and subspecies of turritellas distributed in more than 40 genera and subgenera of 5 subfamilies are known from all over the world. Among 5 subfamilies of the Turritellidae, the Turritellinae is the largest and has a world wide distribution in time and space.

Even though their divergence is fairly wide, their shell morphology is, fortunately enough, very simple, and consists only of spiral cords or seldom spiral beads, and growth-lines on the shell surface, which can be traced back into the early stage of shell growth, the ontogeny of individual specimens.

Since L. GUILLAUME published "Essai sur la classification des turritelles, ainsi que sur leur evolution et leurs migrations, depuis le debut des temps tertiaires" in 1924, several monographic works on the Tertiary turritellas have appeared from several regions of the world. Most authors have tried to establish the phylogenetic trends of regional and/or local groups, for example, ALLISON & ADEGOKE (1960), BADEN-POWELL (1955), BOWLES (1939), IDA (1952), KOTAKA (1954, 1959, 1960), MARWICK (1957) and MERRIAM (1941) and others. Among these, the *Turritella* (*Neohaustator*) *saishuensis-andenensis* Bioseries of Japan established by KOTAKA (*op. cit.*), the *Zeacolpus* (*Stiracolpus*) *kaawaensis-delli* Bioseries (=Group *auct.*) in New Zealand by MARWICK (*op. cit.*), the *Turritella* *moody-cooperi* Bio-

series (= Stock *auct.*) of California by MERRIAM (*op. cit.*) and the *Turritella* (*Haustator*) *tricarinata-communis* Bioseries (= Series *auct.*) of Britain and the Mediterranean by BADEN-POWELL (*op. cit.*) are the most interesting to the writer from the viewpoint of biostratigraphic correlation mainly by means of respective turritellid bioseries.

Previously, the writer (KOTAKA, 1960) pointed out that there is fairly close similarity between each bioseries mentioned above, and concluded:

"... the process of the transformation correspond to each other with high similarity, and can be designated as parallel evolution represented by the appearance and strengthening in the spiral sculpture, and if the age determinations settled by the respective authors are correct, the similar age of the beginning of the transformation in sculpture is recognized... it is noticeable that the complication in sculpture of these turritellid series took place during the late Pliocene and the early Pleistocene, a particular stage in the geological history."

Recent advances in precise biostratigraphic studies of the regions and paleontology of main taxa of the Cenozoic Era, for example, foraminifers, radiolarians, mollusks and diatoms, have called the writer's attention again to the turritellid bioseries of the late Cenozoic. And the writer here proposes to establish the world-wide biostratigraphic correlation and age determination of the late Cenozoic based on the turritellid bioseries.

BRIEF NOTE ON BIOSERIES

In order to facilitate the descriptions of change in spiral ornamentation from species to species in respective bioseries, the writer followed a system of notation previously proposed by MARWICK (1957) and emended by KOTAKA (1959: 59-60) as shown in Figure 1 and the following lines.

"The first spiral generally appears as an angulation on about the adapical third of the whorl and sometimes this

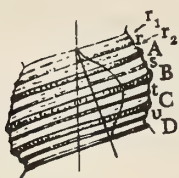


Figure 1

Notation of spiral cord

spiral seems to make the protoconch merge into the first neanic whorls in several forms of the Japanese and New Zealand turritellas, this is designated primary spiral C. The one which appears on about the mid-whorl and the one abapical third of the whorl are designated B and A respectively. A and D are the peri-basal ones. The secondary spirals generally appear abapical to A, between A and B, between B and C, and adapical to C, these are denoted by the small letters r, s, t and u respectively. When the primary spirals become weak, the notation of the primary spirals A, B, C and D are changed into small letters a, b, c and d; when the secondary spirals rival the primary ones, then the secondary spirals, r, s, t and u are changed into capital letters R, S, T and U. Owing to the necessity the notation in the order of appearance of the spirals

can be combined. For example, the notation of the typical *Turritella saishuensis* Yokoyama is shown as (C₁ B₂ s₄ A₃) and the typical *Zeacolpus kaawaensis* (Laws) as (u C B A r). Further, the tertiary spirals appearing in the interspaces between each preceding primary and secondary spirals are shown by a dot (.). If the tertiary spirals are so prominent that they must be noted, then the tertiary spiral appears abapical or adapical to the secondary spiral r is designated r₁ or r₂ respectively, one to secondary spiral s is s₁ or s₂, and so on. In some cases, the spiral threads or striae appear on the surface of preceding spiral A, they may be denoted Ä, and so on."

I. *Turritella* (*Neohastator*) *saishuensis* – *andenensis* Bioseries

Among more than 60 fossil and living species and subspecies of turritellas known from the Japanese Islands and surrounding waters, *Turritella* (*Neohastator*) *saishuensis* Yokoyama has the widest geographic distribution in the late Cenozoic of the Japan Sea borderland. Since Yokoyama described this species from the Pliocene deposits of Cheju Islands of Korea in 1923, the species has long been thought to be an important index fossil of the Pliocene, especially in the oil fields of the Japan Sea borderland, but subsequent authors (IDA, 1952; IKEBE, 1940; KOTAKA, 1954

Table 1

The regional and zonal variants in sculpture of *Turritella cooperi* Carpenter and related species

Species	Age	Notation	Merriam's Pl. & fig.
<i>Turritella cooperi</i> Carpenter	Recent	(u c b s a)	plt. 34, fig. 9.
		(. c . b . a .)	plt. 33, fig. 15.
		(C B A)	plt. 33, fig. 16.
		(C b A)	plt. 33, fig. 14.
	Timm's Point	(C b s a)	plt. 33, fig. 4.
		(C B A)	plt. 35, fig. 14.
		(d C A)	plt. 33, fig. 3.
<i>Turritella margarita</i> Nomland	Santa Barbara	(C B A)	plt. 35, fig. 15.
		(c b A)	plt. 34, fig. 13.
<i>Turritella margarita</i> Nomland	Santa Margarita	(C . . A)	plt. 34, fig. 10.
<i>Turritella carrisaensis</i> Anderson and Martin	Santa Margarita	(C b A)	plt. 34, fig. 3.
		(C . A .)	plt. 34, fig. 2.
		(C A)	plt. 34, fig. 1.
		(. A)	plt. 34, fig. 5.
	(Smooth with shoulders at A and C)		plt. 34, fig. 6.
<i>Turritella moodyi</i> Applin (MS)	Temblor	(Smooth)	plt. 33, figs. 5-7.

"Throughout the long stratigraphic range of the species *T. cooperi* from uppermost Miocene to Recent, little successive change is observed. In nearly all assemblages characteristic regional and zonal variants are found, but certain individuals considered to be more or less typical of the species are found to range throughout, irrespective of stratigraphic or geographic position. In a given assemblage the specifically

typical forms may be present in limited numbers only, most individuals being regional or zonal types. It has been observed that, although a certain complex of variability may characterize the assemblage of a given locality, variants of this complex may occur in other horizons and regions sporadically."

The later half of the statement cited above contains a certain fundamental problem on the classification of fossil communities, and JOYSEY (1956: 85-86) has explicitly explained this problem as follows:

"When dealing with fossils from a geological succession we are faced with a more difficult problem, since it is a continuous series of intermediates. In most cases stratigraphic breaks provide convenient discontinuities, but in the case of a continuous record we are faced with the problem of subdivision for our own convenience. It is unavoidable that the position of the boundaries will be a matter for arbitrary choice, but it is relevant to discuss the direction in which the boundaries should be drawn, this being one of the main problems that the present symposium should endeavor to answer.

The two alternative systems of classification are illustrated in Fig. 1, in which the numbers 1 to 3 represent a series of geological horizons in ascending order. On horizon 1 the symbols *a*, *b* and *c* represent varieties within a single community in which the majority of individuals belong to the typical form "b" while "a" and "c" represent the less common extremes of variation. Similarly, at each horizon the middle letter represents the typical form, and the other symbols represent less usual varieties at this horizon. Ascending the succession, evolutionary change results in a progressive shift in the position of the mode of variation. We now have to decide the direction in which the series is to be subdivided. The boundaries may be defined either on a morphological basis, each of the species having a range, each of the species including the several varieties which formed part of the same community. The size of the categories is arbitrary, and so, for convenience in the following discussion, the two different types of species will be referred to as the variety and the chronological subspecies, respectively."

Careful study of the variants of *Turritella cooperi* (s. l.) (Carpenter) based on sufficient specimens collected from the stratigraphic sequence of the Pacific coast of North America will give us a basis of recognition for the chronological subspecies mentioned above.

Although MERRIAM (1941) did not describe the details of the regional and zonal variants of *Turritella cooperi* and related species, the variants in surface sculpture taken from Merriam's descriptions and illustrations have been tabulated (KOTAKA, 1960), and are reproduced here again. In Table 2 based on our collection of *T. cooperi* from the lower part of the San Pedro Formation of Deadman Island, California (IGPS coll. cat. no. 598) and Table 3 based on the specimens from the Palos Verdes Sand of San Pedro,

Table 2

Variation of the surface sculpture of *Turritella cooperi*
Carpenter from the lower San Pedro Formation.
(IGPS coll. cat. no. 598)

Notation	Number of Specimens
(C b A r)	1
(C B s . A)	2
(C . . A)	7
(C . A)	7
(C A)	3

Table 3

Variation of the surface sculpture of *Turritella cooperi*
Carpenter from the Palos Verdes Sand.
(USGS coll. cat. no. M2017)

Size of the last whorl in mm	Notation
more than 10	(C b . A r) (C b . A .) (C b A) (C . . . A) (. . C B A)
5 - 10	(C . . . A .) (C . . b . . A) (. . C A) (. C . . . A .) (. . . C . b . . A .) (. . C . . . A)
less than 5	(. . C b A) (C) (C . A) (C . A)

California (USGS coll. no. M2017) give us rather precise data on sculptural variation.

It seems to the writer very far from the structural study of a fossil community to draw an urgent conclusion from these tables, but they suggest a tendency of morphological variation of each species indicating a direction of development and even a trend of phylogenetic development of the bioseries in the way of domination and increase in the secondary spirals.

IV. *Turritella (Haustator) tricarinata* – *communis* Bioseries

M. GIGNOUX (1913) first pointed out the phylogenetic relationship between each form of the bioseries in the upper Cenozoic strata of the Mediterranean region, and HARMER (1914-1919) noted that each form belonging to this bioseries has a zonal significance in the British sequence. Then BADEN-POWELL (1954) applied the phylogenetic development of the bioseries to the British sequence and made an attempt to correlate the Pliocene and Pleistocene deposits between Britain and the Mediterranean region.

As shown in Figure 7, the bioseries of the Mediterranean and British forms are represented by the domination and strengthening of the secondary spirals.

According to BADEN-POWELL (1955: 278), the development in sculpture of this bioseries can be described in the following way:

"Not only does the size of the shell increase from *T. tricarinata* to *T. communis*, but also the ornament of three spiral ridges seen in *T. tricarinata* acquires subordinate intermediate ribs in *T. communis* until they are as strong as the original primary ribs and make seven or more ribs of equal size. Gignoux also noted that the *tricarinata* and *pliorecens* forms of ornament can be recognized on the early whorl of the modern individuals of *T. communis*."

BONDI & SANDRUCCI's (1949) statistical analysis on the fossil community of *Turritella (Neohaustator) pliorecens* Monterosato (= *tricarinata* of Bondi and Sandrucci, 1949, *non. auct.*) collected from the Calabrian deposits of Italy also suggests the phylogenetic trend of the bioseries from *T. tricarinata* to *T. communis* through *T. pliorecens*; their statistics are given in Table 4.

Table 4

Variation of the surface sculpture of *Turritella (Haustator) pliorecens* Monterosato from the Calabrian deposits of Italy. (after BONDI & SANDRUCCI, 1949)

Class	Number of Specimens
3	8
4	10
5	46
6	132
7	139
8	156
9	95
10	35
11	16
12	14

In Table 4, the class represents the number of the whorl on which the first intercalary spirals or secondary spirals begin to appear, that is, according to Bondi and Sandrucci, the specimens included in the first three classes are allocated to the typical *Turritella communis*, and these of the last three to the typical *T. tricarinata*. Although they lumped up these forms into one species of *T. tricarinata*, and considered them to be of varieties because of their continuous change in sculpture, the writer believes that this community from the Calabrian should be allocated to the species of *T. pliorecens* according to the mode given by the frequency of morphological variations in the community, thus, the phylogenetic trend of the bioseries can be easily recognized from the viewpoint of population structure.

CONCLUDING REMARKS

All of these phylogenetic series or bioseries described above are exhibited by progressive increases in density and strength of secondary and tertiary spiral sculpture. This analogy seems to be a phenomenon of parallel evolution taking place contemporaneously in each regional or local bioseries.

And further, sudden and considerable change in sculpture in each bioseries is detected across the Pliocene-Pleistocene boundary shown as a broken line in Figure 3.

AGE	JAPAN	NEW ZEALAND	CALIFORNIA	ITALY
HOLOCENE			<i>cooperi</i> (u c b s a)	
	<i>andenensis</i>	<i>delli</i>		<i>p. communis</i>
	<i>otukai</i>	<i>d. murdochi</i>		
PLEISTOCENE	<i>s. etigoensis</i> (..C...B.S.A.r)	<i>d. vellai</i> (u C . B A r)	<i>cooperi</i> (C B A)	<i>pliorecens</i> (u Ct B . S . Ar.)
PLIOCENE	<i>saishuensis</i> (s.s.) (C B s A)	<i>kaawaensis</i> (u C B A r)	<i>c. paucisculpta</i> (C b A)	<i>tricarinata</i> (u C . B A r)
			<i>c. fernadoensis</i> (c . . a)	
	<i>s. motidukii</i> (C B A)			
MIOCENE			<i>margaritana</i> (C . A)	
			<i>carrisaensis</i> (C A)	
			<i>moodyi</i> ()	

Figure 3

Correlation table of 4 turritellid bioseries

At the present, although the physiological significance and mechanism of development in spiral ornamentations are not yet fully known, it can be emphasized that the world-wide decline of marine water temperature and/or shallowing of the marine realm caused by world-wide sea level change are reflected by sudden changes in sculpture, and this boundary roughly corresponds to the Neogene-Quaternary boundary when the world-wide ice-sheets started to develop.

In Italy, this boundary can be drawn between the Astian and Calabrian stages, that is, at the generally accepted Neogene-Quaternary boundary. In the New Zealand bio-series, this boundary corresponds to that of the Waitotaran and Nukumaruan Stages. And HORNIBROOK (1977) in summarizing the age determination of the New Zealand stages, put the Neogene-Quaternary boundary at the top of the Mangapanian Stage or the Waititaran Stage of old sense mainly by means of planktic foraminiferal ranges. His Neogene-Quaternary boundary is quite safely assigned to the boundary between the *Stiracolpus kaawaensis* and *S. delli vellai* zones in the stratotype sequence of the Waitotaran and Mukumaruan Stages along Wanganui Beach of North Island, New Zealand.

But placement of the Neogene-Quaternary boundary in Japan is still controversial; for example, IKEBE *et al.* (1977)

put this boundary at the base of the Kitaura Formation correlative of the Tentokuji Formation in Figure 2, mainly based on a magnetostratigraphic event and the last occurrence of the planktic foraminifer *Globoquadrina asanoi*. At the same time, they noted that discrepancies still exist in age and correlation, especially with the scheme of molluscan biostratigraphers.

According to ADDICOTT (1977), the Neogene-Quaternary boundary in California has not been drawn strictly, but it seems to the writer that the boundary in question can still be drawn on at the base of the San Pedro Formation including the Timms Point Siltstone Member of recent sense as already shown by MERRIAM's text-figure (1941: 49, fig. 8) cited above.

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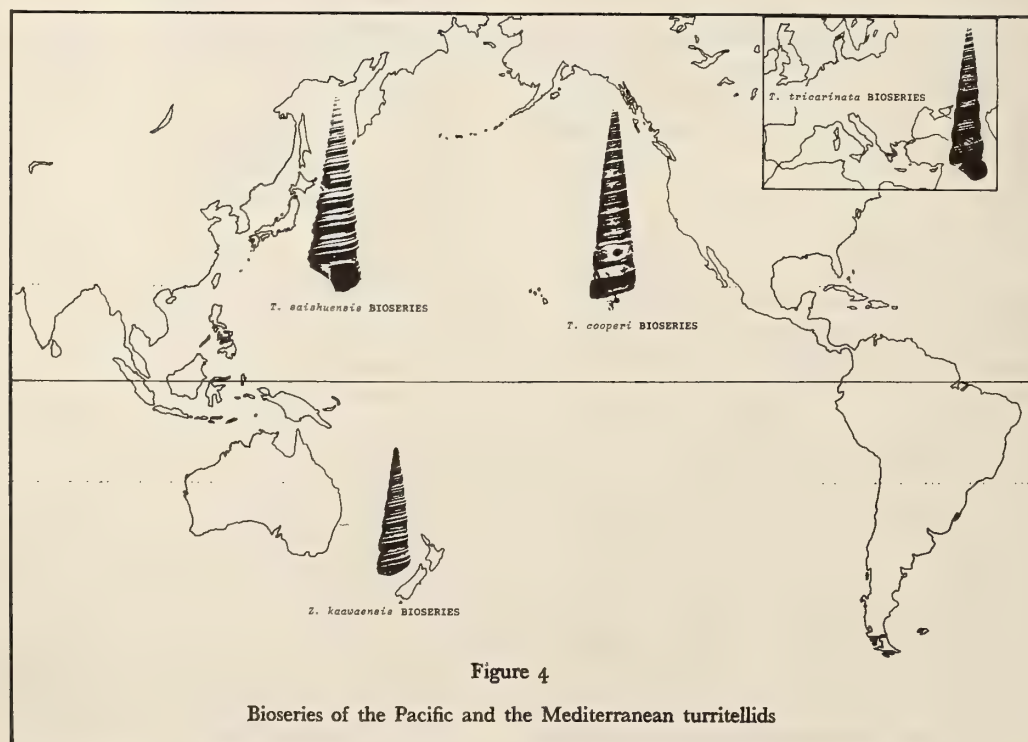


Figure 4

Bioseries of the Pacific and the Mediterranean turritellids

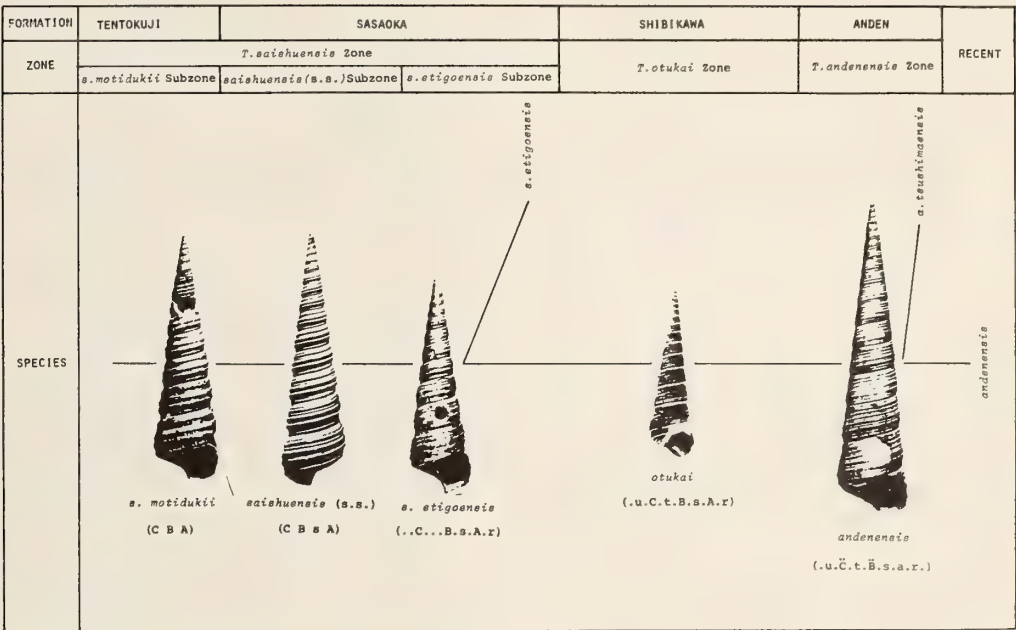


Figure 5
Phylogeny of *Turritella* (*Neohastator*) *saishuensis* – *andenensis*
Bioseries in Japan

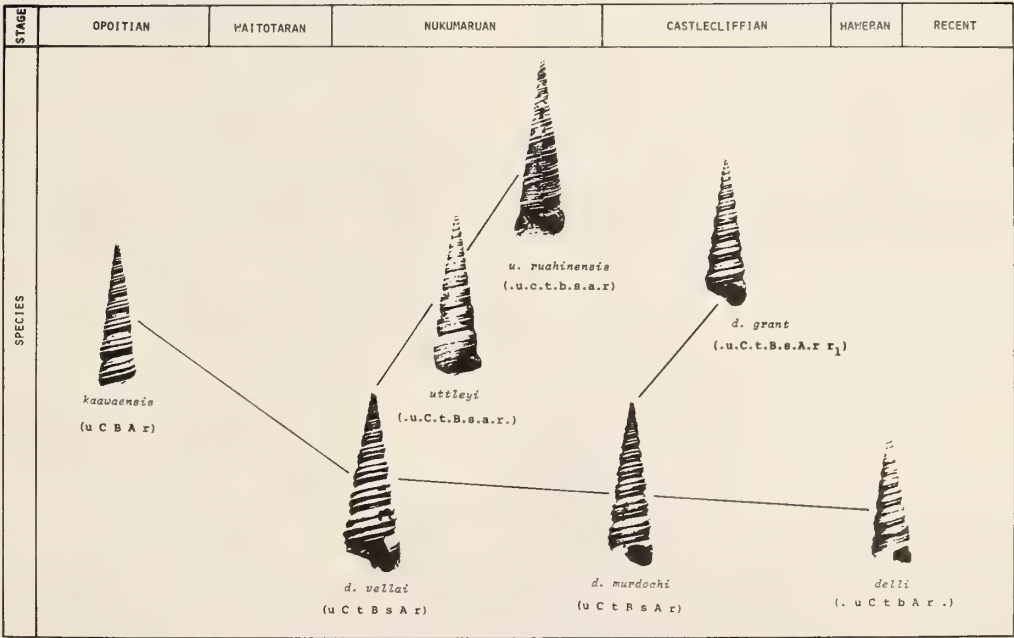


Figure 6
Phylogeny of *Zeacolpus* (*Stiracolpus*) *kaawaensis* – *delli* Bioseries
in New Zealand

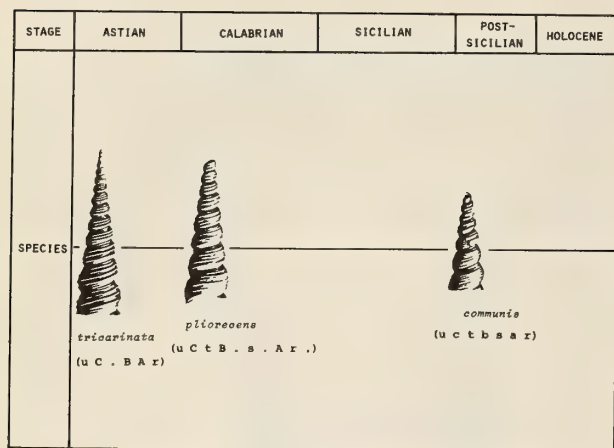
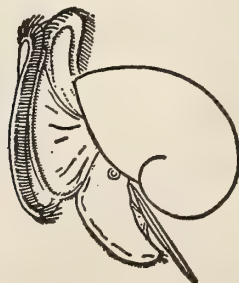


Figure 7

Phylogeny of *Turritella* (*Haustator*) *tricarinata* - *communis*
Bioseries in Italy

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Neogene Pectinidae of the Northern Pacific

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(1 Text figure)

INTRODUCTION

IT IS WELL KNOWN that the Neogene Pectinidae is one of the most important groups of mollusks for age determination and correlation of Neogene strata because of their rather short geological range and also because they are the largest group of fossil marine mollusks. The long duration from spawning through the pelagic and sessile stages to the free swimming stage favors wide dispersal, colonization of new habitats and, consequently, speciation. Also, as the pectinid shells are usually rather well preserved even when the majority of the associated shells are represented as molds or casts, their collection and identification is facilitated. Therefore, they are good tools for interregional correlation.

Among the Neogene pectinids of the Northern Pacific region *Patinopecten*, *Mizuhopecten*, *Yabepecten*, *Swiftpecten*, *Fortipecten* and *Chlamys cosibensis* (Yokoyama) are considered to be significant for interregional correlation between Eastern Asia and North America because they are known from the Japanese Islands, Sakhalin, Kamchatka, Alaska and the West Coast of North America. Also, the genus *Amussiopecten* is considered to be one of the most interesting and significant pectinids particularly from the viewpoint of its world wide distribution.

In the present article remarks on the above mentioned Neogene pectinids of the Northern Pacific are given and paleontological significances are also discussed.

NOTES ON PECTINIDS OF THE NORTHERN PACIFIC

1) *Patinopecten* and *Mizuhopecten*

The genus *Patinopecten* is one of the most interesting Cenozoic pectinids of the eastern North Pacific, because it is abundant in species, shows a wide range of morphological characters and has a rather restricted geological range.

Patinopecten was established by DALL (1898) as a section of the genus *Pecten* based upon *Pecten caurinus* Gould, a common Recent scallop of the eastern North Pacific. Thenceforth, *Patinopecten* has frequently been recorded from the Recent seas of the Northern Pacific and from the Tertiary and Quaternary deposits of western North America, the Japanese Islands, Sakhalin, and Kamchatka, but not from elsewhere. From a study of the so-called *Patinopecten* of Japan the writer (MASUDA, 1963) pointed out that all of the Japanese fossil and Recent species of the so-called *Patinopecten* differs from the true *Patinopecten* of North America and he proposed the new genus *Mizuhopecten* for most of the species of the so-called *Patinopecten* of Japan, based upon *Pecten yessoensis* Jay, a common Recent scallop of Northern Japan.

Also, according to the writer's study (MASUDA, 1971a), it became evident that among the species described from the West Coast of North America *Pecten* (*Patinopecten*) *bakeri* Hanna and Hertlein (1927), *Patinopecten bakeri diazi* Durham (1950a) and *Patinopecten marquerensis* Durham (1950a) described from the Pliocene strata of Baja California, Mexico, should be removed from *Patinopecten* and placed in the newly proposed genus *Leopecten* based upon *Pecten* (*Patinopecten*) *bakeri* Hanna and Hertlein. Moreover, it became evident that *Patinopecten* (*Mizuhopecten*) *skonnunensis* MacNeil (1967) can not be referred to *Mizuhopecten*; but *Patinopecten* n. sp. illustrated by ADDICOTT (1966) from the Montesano Formation in Washington was described by the writer as a new species of *Mizuhopecten* (MASUDA, 1971a).

The typical *Patinopecten* is specifically abundant during the Tertiary Period in western North America but only one Recent species is known—*P. caurinus* (Gould) which occurs north of San Francisco Bay. *Patinopecten* has been usually considered as a cool water indicator of the West Coast of North America. MACNEIL (1967) stated that most molluscan stocks on the West Coast of North America have older representatives in the Japanese Islands. However, as the writer pointed out (MASUDA, 1963, 1971a), it is evident

that the ancestral stock of *Patinopecten* is not a migrant from Asia but probably from the Mediterranean region.

In Japan the genus *Mizuhopecten*, ranging from the Oligocene to the Recent, is very abundant specifically and individually. But there are only two species known in the Pleistocene and only one from the Recent seas of Northern Japan. It seems probable that the majority of the *Patinopecten* species recorded from Sakhalin and Kamchatka should be referred to *Mizuhopecten*, and that *Patinopecten* may not be found in the western Pacific borderland.

In general, the water temperature gradually lowered from the early to latest Neogene in the Circum Pacific (DURHAM, 1950b, MASUDA, 1963a, 1973b, ADDICOTT, 1969), and the decrease in number of *Patinopecten* or *Mizuhopecten* species besides other pectinids during the Tertiary to the Recent may coincide with the lowering of the water temperature. It seems that the decrease in the pectinids on both sides of the Northern Pacific with advance of geological time may be explained by the changes of environmental conditions.

2) *Yabepecten*

Yabepecten established by the writer (MASUDA, 1963) based upon *Pecten tokunagai* Yokoyama from the Pliocene Koshiba Formation in Kanagawa Prefecture, can be considered to be potentially significant in interregional correlation because of its restricted geological range and wide geographical distribution.

MASUDA & ADDICOTT (1970) pointed out that *Pecten* (*Amusium*) *condoni* Hertlein from the Montesano Formation of western Washington, is a *Yabepecten* and not an *Amusium*. This was the first record of *Yabepecten* in the Tertiary of eastern North Pacific. *Yabepecten* is restricted to early Pliocene formations of Northern Japan. Judging from the associated fauna, the early Pliocene formations of Northern Japan were deposited under cool water conditions. And, from the fauna associated with *Y. condoni* in the Montesano Formation, a probable early Pliocene age is suggested. Owing to its geological record and its wide geographical distribution, it is of considerable significance in Circum North Pacific faunal correlation. It is expected that *Yabepecten* will be found from Sakhalin, Kamchatka, Alaska and other areas along the Eastern Pacific.

3) *Swiftopecten* and *Nanaochlamys*

In 1935 HERTLEIN proposed *Swiftopecten* for *Pecten swiftii* Bernardi, a common Recent scallop of Northern Japan. Also *Nanaochlamys* was established by HATAI & MASUDA (1953) based upon *Pecten notoensis* Yokoyama

from the Miocene Nanao Formation, Ishikawa Prefecture, Japan.

As known at present the oldest occurrence of *Swiftopecten swiftii* (Bernardi) is the middle Miocene formations of Northern Japan, where it is rather rare (MASUDA, 1959a). The associated molluscan fauna mainly comprises temperate water elements. But with the progress of geological age *S. swiftii* gradually increased its dominancy with the increase of cooler water mollusks from the middle Miocene through Pliocene to Recent (MASUDA, 1959a, 1972).

As pointed out by the writer (MASUDA, 1960), *Swiftopecten swiftii* branched off from *Nanaochlamys notoensis* (Yokoyama) in the middle Miocene. The morphological characters of *N. notoensis*, *N. notoensis otutumiensis* and *S. swiftii* closely resemble each other in their younger stage, but with growth the surface sculpture in the adult stage becomes considerably different. The surface sculpture in the younger stage of *N. notoensis* is retained in the adult stage of *N. otutumiensis* and *S. swiftii*, but the surface sculpture in adult stage of *N. notoensis* is not observed in that of the latter. And, *N. otutumiensis* and *S. swiftii* occur from a geological horizon higher than that of *N. notoensis*. Therefore, it is inferred that *N. notoensis* is ancestral to *N. otutumiensis* and *S. swiftii*, that is to say, *N. otutumiensis* and *S. swiftii* branched off from *N. notoensis* in the middle Miocene and they represent parallel forms of generic distinction. During the early Miocene *N. notoensis* was a warm water inhabitant as shown from the associated fauna. But it became extinct probably owing to the diverse environmental conditions at the end of the early Miocene. *Nanaochlamys otutumiensis* and *S. swiftii* branched off from *N. notoensis* in the late early Miocene. *Nanaochlamys otutumiensis* became extinct by the influence of rather cool water conditions of the late Miocene, but *S. swiftii* survived to the Recent with little morphological variations. Consequently, the factors controlling the evolutionary change in the *N. notoensis* group were probably due in part to the difference of environmental conditions. *Nanaochlamys notoensis* and *N. notoensis otutumiensis* are not known from Sakhalin, Kamchatka and Alaska.

The first appearance of *Swiftopecten* along the West Coast of North America is in the Yakataga Formation in Alaska, which yielded *S. donmilleri* (MACNEIL, 1967; KANNO, 1971). It is thought that the occurrence of *Swiftopecten* along the West Coast of North America is a result of its migration from Asia to North America. Therefore, the writer considers that the Yakataga Formation in Alaska is at least not older than the middle Miocene formations in Japan. *Swiftopecten swiftii* extended its distribution to Northern California in the early Pliocene and *S. swiftii parmeleei* (Dall) which is known from Central to Southern

California, branched off from the *S. swiftii* stock as a result of its southward migration followed by localization and adaptation in the middle Pliocene and it became extinct at the end of middle Pliocene. On the other hand, with progress of geological age *S. swiftii* retreated to Alaska and became extinct in the Pleistocene. Therefore, it is expected that *S. swiftii* will be found from the Pliocene and Pleistocene formations of the northern part of western North America (MASUDA, 1972).

As already stated by the writer (MASUDA, 1959a), some morphological differences such as concentric constrictions or the nature of the radial ribs of the left valve in *Swiftopecten swiftii* are observed between specimens living in the northern areas and those living in more southern areas. These morphological features suggest that the specimens living in the northern areas are somewhat less influenced by the water temperature than those living in more southern areas. And, the morphological differences observed between the fossil and Recent specimens may be the reflection of the environmental conditions such as water temperature. From such inferences it may be interpreted that the so-called *S. kindlei* represents the northern type of *S. swiftii* and that some of the so-called *S. parmeleei* from northern California represent the southern type of *S. swiftii*. Also, the so-called *S. donmilleri* may represent the southern type of *S. swiftii*. Therefore, it can be considered that the Yakataga Formation that yielded *S. swiftii* may have been deposited under the influence of temperate to cool water environmental conditions. Although the geological age of the Yakataga Formation is now open to question, the writer is inclined to consider that a part of the Yakataga Formation may represent the late Miocene or very early Pliocene.

4) *Fortipecten*

Since YOKOYAMA (1930) described *Pecten takahashii* from the Pliocene Maruyama Formation in South Sakhalin, the species was frequently recorded from the Pliocene formations in Japanese Islands and Sakhalin. In 1940 YABE & HATAI established the genus *Fortipecten* based upon *P. takahashii* Yokoyama.

The genus *Fortipecten* has hitherto been considered to be an important Pliocene pectinid of Northern Japan, until KOTAKA & NODA (1967) described *F. kuroishiensis* from the middle Miocene Ogawara Formation, Aomori Prefecture, Northern Honshu, Japan. Among three species of *Fortipecten*, *F. takahashii*, *F. kuroishiensis* and *F. kuroishiensis*, known from the Japanese Islands, *F. takahashii* is the most important species, particularly from the viewpoint of its restricted geological range and very wide

geographical distribution from middle Northern Honshu northward to Hokkaido and Sakhalin and Kamchatka (MASUDA, 1962b).

On the other hand, several species such as *Fortipecten takahashii*, *F. pilutunensis*, *F. sachalinensis*, and *F. mironovi*, have been described from North Sakhalin and Kamchatka (KHOMENKO, 1931; SLODKIEWITSCH, 1938; ILYNA, 1963; KRISHTOFOVICH, 1964). And *F. hallae* (Dall) (MACNEIL, 1943) and *F. mollerensis* MacNeil (1967) have been described from Alaska. Therefore, the occurrence of *Fortipecten* in the Circum North Pacific is a result of migration from the Japanese Islands. However, those mentioned species are in need of further study to clarify their taxonomic relations. For example, according to the present writer's study based upon the holotype and topotype of *F. mollerensis* MacNeil, it is evident that MacNeil's *mollerensis* is different from *Fortipecten* and should be referred to *Mizuhopecten*.

5) *Chlamys cosibensis* (Yokoyama)

Chlamys cosibensis was first described by YOKOYAMA (1911) from the Pliocene Koshiba Formation, Kanagawa Prefecture. Thenceforth, this species has been frequently recorded from the Miocene to Pliocene formations of Japan and its adjacent areas.

The first occurrence of *Chlamys cosibensis* (Yokoyama) is in the middle Miocene of Northern Japan and at that locality the associated molluscan fauna consists mainly of temperate water elements. The ancestral form of *C. cosibensis* (s. s.) is considered to be *C. cosibensis hanzawae* Masuda (1959b) which is known from the early Miocene formations of Japan, where it occurs in association with warm water mollusks. With the progress of geological age *C. cosibensis* (s. s.) increased its dominance in association with an increase of cooler water mollusks from the middle Miocene to early Pliocene. *Chlamys cosibensis* (s. s.) has been frequently recorded from the early Pliocene formations of the Japan Sea borderland and the Kwanto region (MASUDA, 1962b). It has been recorded from North Sakhalin and Kamchatka (SLODKIEWITSCH, 1938; ILYNA, 1963; KRISHTOFOVICH, 1964, 1969). Also, as pointed out by the writer (MASUDA, 1973a) MacNeil's *C. (Swiftopecten) leohertleini* from the Pliocene Tachilni Formation at the western end of the Alaska Peninsula (MACNEIL, 1970) is a synonym of *C. cosibensis* (s. s.). Moreover, MACNEIL (1973) illustrated *C. (Swiftopecten) donmilleri* MacNeil from the Unga Conglomerate Member of Bear Lake Formation, Alaska Peninsula, but according to the writer's study of the specimens preserved in the collections of the California Academy of Sciences, San Francisco and Re-

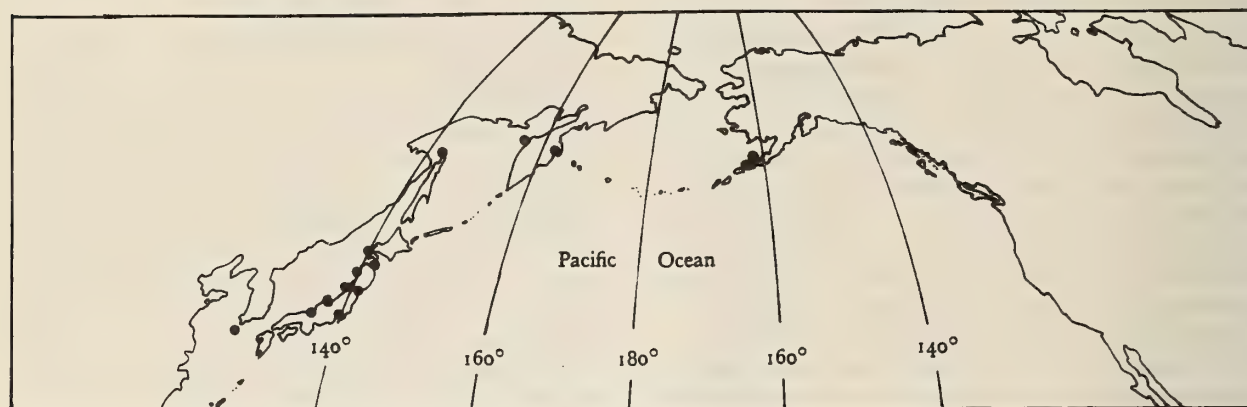


Figure 1

Geographical Distribution of *Chlamys cosibensis* (Yokoyama)

search Center of Amoco Production Company, Tulsa, from the same locality as MacNeil's *C. donmilleri*, it is evident that MacNeil's *C. donmilleri* is a synonym of *C. cosibensis* (s. s.), because the morphological characters are quite similar with those of *C. cosibensis* (s. s.). The geographical distribution of *C. cosibensis* (Yokoyama) is shown in Text figure 1.

The writer pointed out (MASUDA, 1973a) that the size of *Chlamys cosibensis* (s. s.) from middle Miocene formations is usually smaller than those from Pliocene formations and also that the radial ribs of the Miocene specimens are generally somewhat more distinct and somewhat higher than those of the Pliocene forms. Therefore, based upon morphological characters the geological age of the *C. cosibensis* (s. s.) bearing formations can be determined, and correlation of the geographically isolated formations can be undertaken. Since *C. cosibensis* (s. s.) from Alaska (MACNEIL, 1970, 1973; MASUDA, 1973a), Sakhalin (ILYNA, 1963) and Kamchatka (SLODKIEWITSCH, 1938, KRISHTOFOVICH, 1969; MASUDA, 1973a) are of the Pliocene type of morphology, the writer considers that their occurrence is a result of migration from the Japanese Islands via Kamchatka to Alaska during the early Pliocene, although MACNEIL (1973) assigned the Unga Conglomerate Member of Bear Lake Formation in Alaska Peninsula to the early Middle Miocene.

6) *Amussiopecten*

Amussiopecten has been frequently recorded from various localities in Neogene and Paleogene formations in South and Central Europe, the Mediterranean Region,

Iran, East Africa, Madagascar, South East Asia and East Asia, but no species has been described and recorded under *Amussiopecten* from either North America or South America. But according to the writer's study (MASUDA, 1971b) it became evident that several species from the Oligocene and Miocene formations along the West Coast of North America, Central America, the Caribbean Region and northern South America, should be referred to the genus *Amussiopecten*. And all species of *Amussiopecten* in Europe, Africa and America became extinct at the end of the middle Miocene, but three species of *Amussiopecten* in East Asia survived to the Pliocene.

In general, the decrease in number of species with time can be explained by the changes in oceanographic environmental conditions. Therefore, as the result of these changes all species of *Amussiopecten* in Europe, Africa and America became extinct at the end of middle Miocene but in East Asia three species were able to survive to the early Pliocene. That is to say, the environmental conditions in East Asia have been more stable than those of the other areas from the early Miocene to the early Pliocene. From the accounts given above it appears that the distribution of *Amussiopecten* has been dependent upon progressive changes in oceanographic conditions during its geological range. Therefore, world wide occurrences of *Amussiopecten* are considered to be very significant for interregional correlation.

The late Oligocene to Middle Miocene pectinids in North America are usually composed of European elements, but the Late Miocene to Pliocene pectinid fauna of the northern West Coast of North America generally contains a mixture of Asian elements, the survivors of Miocene

pectinids and endemic genera. But along the southern West Coast of North America, the East Coast of North America and in the West Indies, the pectinid faunas differ greatly from those of the northern West Coast since the late Miocene. Along the southern West Coast the Pliocene pectinid fauna reveals a quite different aspect from those of northern part. These faunal provinces indicate geographic differentiation.

CONCLUDING REMARKS

The occurrences of the Japanese pectinids such as *Mizohopecten*, *Yabepecten*, *Swiftiopecten*, *Fortipecten*, *Amusiopecten* and *Chlamys cosibensis* in the Neogene formations of the northern part of the West Coast of North America are significant for Circum Pacific correlation of the Neogene formations.

In general, there are two periods of remarkable development of the Pectinidae in the Tertiary of Japan (MASUDA, 1962b). These two periods mark the abrupt appearance of genera and subgenera, extreme individual variability and species differentiation. The two unstable periods are represented by the early Miocene and early Pliocene ages (MASUDA, 1962b; 1973b). Such remarkable features are also recognized in the Pectinidae of the "Vaqueros" and "Jacalitos" stages of the West Coast of North America (ARNOLD, 1906; ADDICOTT, 1974), and also in the Japanese Turritellidae (KOTAKA, 1959), Arcidae (NODA, 1966) and others.

The Miocene Pectinidae of Japan can be classified into early, middle and late Miocene (MASUDA, 1962b). As stated earlier, during the early Miocene, the Pectinidae were abundant in species and individuals, showed a wide variety of sculpture and possessed a rather restricted chronological distribution. The early Miocene Pectinidae of Japan had a rather wide geographical distribution and was represented by the *Nanaochlamys notoensis* assemblage zone. In the middle Miocene the pectinid fauna became more varied, being represented in Northern Japan by the shallow water *Miyagipecten matsumoriensis* assemblage and the *Mizohopecten kimurai* assemblage. In Southern Japan the pectinid fauna is represented by the *Amusiopecten akiyamae* assemblage, whereas in Central Japan there is a mixed pectinid assemblage consisting of the elements of Southern Japan and Northern Japan. Although the late Miocene pectinids are characterized by the mixed assemblage of the survivors of the earlier horizons and the appearance of some Pliocene species, their detailed characters are not well known, because of the restricted distribution of the pectinid-bearing formations.

Another development of the Pectinidae is recognized at the beginning of the Pliocene age in Japanese Islands. The early Pliocene is characterized by the *Yabepecten tokunagai* assemblage in the Japan Sea borderland and Kwantō region, the *Fortipecten takahashii* assemblage in the Northern Pacific borderland and the *Amusiopecten praesignis* assemblage in the Southern Pacific borderland. Among the early Pliocene pectinid assemblages, the *F. takahashii* assemblage can be traced from Northern Japan through Sakhalin to Kamchatka and the *Y. tokunagai* assemblage from Japan to the Alaska Peninsula. The *A. praesignis* assemblage can be traced from Central Japan to Taiwan and tends to change northwards gradually to the *Y. tokunagai* assemblage. The *Y. tokunagai* and *F. takahashii* assemblages may have been controlled within the same sedimentary province by ecological and other conditions.

Consequently, it is reasonable to correlate the early Pliocene formations of the Japanese Islands with the Pomyr Series in North Sakhalin, the Upper Kavran and Etronskaja Series in Kamchatka, the Tachilni Formation and Unga Conglomerate in Alaska, and also with the Montsano Formation in Washington. The mentioned correlation of the Pliocene formations in the Northern Pacific area is also supported by the other molluscan faunas.

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Neptunea

(Gastropoda : Buccinacea)

in the Neogene of the North Pacific and Adjacent Bering Sea

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(2 Plates; 9 Text figures)

INTRODUCTION

THE FRIGIOPHILIC, large gastropod *Neptunea* Röding, 1798, ex Bolten MS, a scavenger and facultative predator, is a conspicuous, common element in arcto-boreal, inshore benthic faunas of the late Cenozoic in the Northern Hemisphere. GOLIKOV (1963) and NELSON (1974) revised the taxonomy of living and fossil *Neptunea*, and established it as a more modern genus than portrayed previously. *Neptunea*, indigenous to the western North Pacific, evolved in waters off northern Japan and Sakhalin during the early Oligocene. It is distributed widely in post-early Miocene, outer sublittoral to upper bathyal molluscan faunas north of 32° N in the North Pacific and adjacent Bering Sea. Although entirely epifaunal crawlers after hatching, the spatial distribution of *Neptunea* mirrors those of *Fusitriton* and *Mya* which have pelagic larvae. Its distinctiveness, abundance, taxonomic diversity, widespread geographic distribution, and relatively rapid evolution make *Neptunea* a key element in the biochronology of upper Cenozoic strata in the boreal North Pacific. Distinctive spiral sculpture on early adult whorls of *Neptunea* distinguishes three subgenera, and four stocks within *N. (Neptunea)*, each of which displays a distinctive phyletic and zoogeographic pattern. *Neptunea (Golikovia)* and *N. (Neptunea)* were distinct taxonomically by the late Oligocene. *Neptunea (Sulcosipho)* evolved from, or shares a common ancestry with, *N. (Neptunea)* in the late Oligocene or earliest Miocene.

GENERAL MORPHOLOGY

Neptunea (Neptunea) antiqua (Linnaeus, 1758), the type species from the eastern North Atlantic (NELSON, 1976), exhibits the basic shell form of the genus (GOLIKOV, 1963: pl. XXIII, fig. 12; PEARCE & THORSON, 1967: text figs. 1-3; NELSON, 1974: pl. 53, figs. 1, 3). Species of *Neptunea* have shortened to moderately elongate fusiform, dextrally-coiled, adult shells of 50 to 200 mm or more in length. Sinistral shells are rare.

Well-developed spiral sculpture, often of three or four orders of strength, typifies *Neptunea*. Ontogenetic changes involve differential development of subordinate spiral elements. These shells lack alternation of spiral, axial, or reticulate sculpture.

Descriptive Notation of Spiral Sculpture

In a descriptive notation modified from that used for turritellids by MERRIAM (1941), KOTAKA (1959), and ALLISON (1965), the primary spiral rib (first order of strength) at the shoulder of the initial adult (or teleoconch) whorl is denoted "B." Visible spirals anterior (abapical) to "B" on that whorl are in succession "C," "D," "E," *et seq.* Equivalent lower case letters denote reduced development of these ribs. Letters enclosed by parentheses indicate that these spiral elements may be absent in some specimens of the taxon. "A" or "a" designates the primary spiral rib on the

subsutural shelf or ramp. Unlike turritellids, no primary ribs originate anteriorly to "B" on the younger whorls of the adult shell. Subscript numerals indicate the whorl on which the spiral elements originate. Axial sculpture (lobes, lamellae, and varices, but never ribs) is absent or rare, and when present is confined usually to posterior (adapical) whorls.

Subgenus-Group Taxa

Despite the highly developed polymorphism within *Neptunea*, consistently recognizable subgenera were defined using the notation, configuration, and relative position (distance from the posterior suture of the whorls) of the primary spiral sculpture on the initial adult whorl of the shell. These characters were supplemented by the shape of the shells, especially the whorl profiles and proportions of shoulders and subsutural areas.

The notation and configuration of primary spiral ribs on initial and subsequent adult whorls delimit three subgenera of *Neptunea*, including *N. (Golikovia)* Habe and Sato, 1972, *N. (Sulcosipho)* Dall, 1916, and *N. (Neptunea)*. These characters permit the identification of incomplete specimens. A strong, semireticulate pattern of spiral and axial ribs on the initial adult whorls in *N. (Barbitonia)* Dall, 1916, and the unique microstructure of its shell (Togo, 1974: 378-379), not shared by other *Neptunea*, indicate that the subgenus should be elevated to full generic rank and reassigned to the Buccinulidae. One hundred and thirty species of Cretaceous to Holocene "*Neptunea*" were reassigned to other caenogastropod genera in the most recent taxonomic revision of the genus (NELSON, 1974: Ap-

pendix B). Thus, *Neptunea* comprises 61 species—and sub-species—group taxa, including 31 extinct and 7 new taxa. This taxonomic revision and that of GOLIKOV (1963) facilitate evaluation of the chronostratigraphy and zoogeography of *Neptunea* during the Neogene.

ANCESTRY

Neptunea, indigenous to the North Pacific, was thought to have evolved from a late Paleocene or Eocene complex also ancestral to *Brucarkia* or *Molophophorus* (Melongenidae) and *Siphonalia* (Neptunidae) (ILYINA, 1963: 99; GOLIKOV, 1963: 40; text fig. 59; KRISHTOFOVICH, 1964: 8-9; text fig. 1; STRAUCH, 1972: 173, based on Golikov; and GOLIKOV & TZVETKOVA, 1972: 2; text fig. 1). However, the morphological specializations evident in the earliest species of these genera preclude their consideration as codescendant forms. Instead, *Neptunea* originated in the Oligocene from a complex also ancestral to *Ancistrolepis altispinata* (NAGAO, 1928), the latter based on a single specimen from the Doshi Formation (provincial lower Oligocene) of Hoshuyama, Fukuoka Prefecture, northern Honshu. *Ancistrolepis altispinata* exhibits the most generalized morphology of any Eocene or Oligocene Japanese species referred by investigators to *Neptunea* or to its junior objective synonym *Chrysodomus* Swainson, 1840 (see OYAMA, MIZUNO & SAKAMOTO, 1960: 59-68 and Appendix B; MACNEIL, 1973: 119; and NELSON, 1973: 85; 1974: 45-46; and 1977: 375). Although details of the primary sculpture on the initial adult whorl and the apertural characters of *A. altispinata* are unknown, the distinctly angulate base of the body whorl is a distinguishing character in *Ancistrolepis*. Of the

Explanation of Figures 2 to 7

(all Figures $\times 1$ unless otherwise noted)

Figure 2: *Neptunea (Neptunea) pluricostulata* Ilyina. UCMP 14530. UCMP loc. D3712, ex Central Scientific-Research Geological Exploration Museum Academician F. M. Chernyshev (CNIGR), Leningrad, U. S. S. R., courtesy of Yuri Gladenkov and Oleg Petrov. Etolon Formation, upper Miocene. Point Nepropusk, Kamchatka.

Figure 3: *Neptunea (Neptunea) uncostulata* Ilyina. UCMP 14531. UCMP loc. D3712, ex CNIGR. Etolon Formation, upper Miocene. Point Nepropusk, Kamchatka.

Figure 4: *Neptunea (Neptunea) borealis* (Philippi). CNIGR 3829/2. Ol'khov Formation, lower Pleistocene. Ust' Kamchatsk, Kamchatka. $\times 1.5$

Figure 5: *Neptunea (Neptunea)* sp. A. aff. *N. (N.) lyrata* (Gmel-

lin). CNIGR 3586/1818/22. Limintev Formation, lower Pliocene. Karagin Island, U. S. S. R.

Figure 6: *Neptunea (Neptunea) lyrata altispina* (Gabb). USNM 250502 (Catalog No. 36), rubber cast. USGS Cenozoic loc. M1876. Yakataga Formation, upper Miocene part. Chaix Hills, Malaspina district, Alaska.

Figure 7: *Neptunea (Neptunea) lyrata altispina* (Gabb). UCMP 14532. UCMP loc. B7879. Rio Dell Formation¹, upper Pliocene. Humboldt County, California.

¹ OGLE's (1953) Wildcat Group and its five formations (ascending: Pullen, Eel River, Rio Dell, Scotia Bluffs, and Carlotta) are adopted herein for U. S. Geological Survey usage. The biochronology of the Wildcat formations was refined by FAUSTMAN (1964).



Figure 2

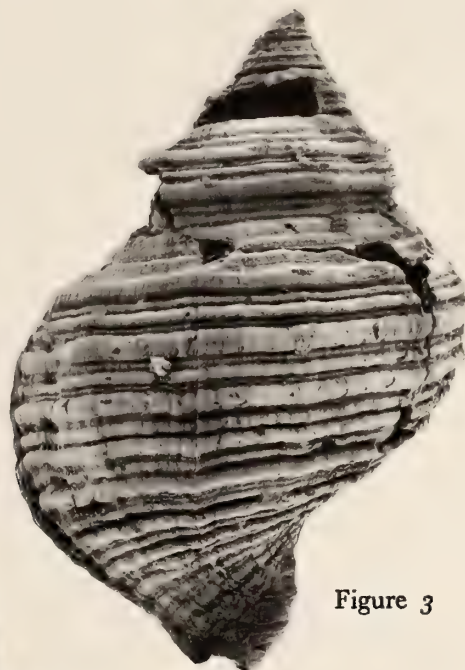


Figure 3

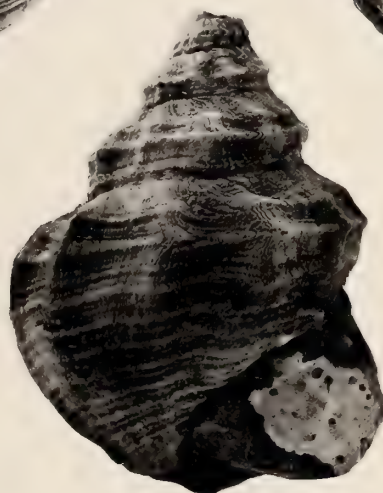


Figure 4



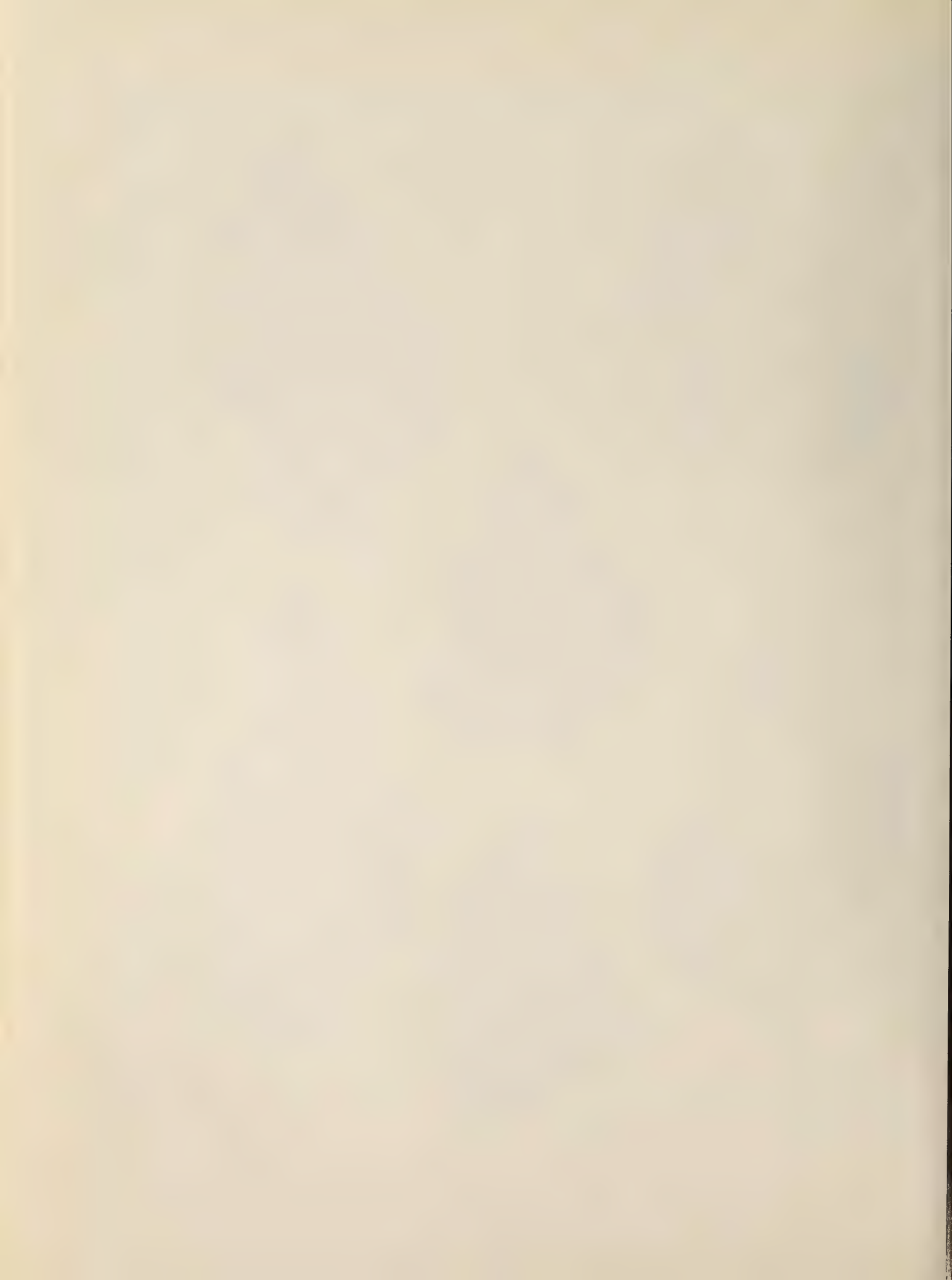
Figure 5



Figure 7



Figure 6



other Eocene or Oligocene Japanese species of supposed *Neptunea*, only *N. (N.) modesta* (Kuroda in Homma, 1931) remains within the genus (NELSON, 1974: 46).

Early Species in the North Pacific

Neptunea originated and evolved in waters off northern Japan and Sakhalin in a low-boreal environment during the early to middle Oligocene. During that episode of climatic deterioration (ADDICOTT, 1969, 1970; INGLE, 1977), natural selection produced greater efficacy of reproduction in increasingly cooler waters. Descendants migrated northward during the late Oligocene to middle Miocene amelioration, when water temperatures off northern Japan and Sakhalin during the coldest part of the spawning seasons became too high for successful breeding.

Many of the Oligocene and Miocene species referred uncertainly to *Neptunea* are based on specimens that lack preserved initial adult whorls. *N. (Neptunea) modesta* (Kuroda in Homma), of the *N. (N.) pribiloffensis* (Dall) stock, occurs in the Nenokami Sandstone (upper Oligocene) of Yoshida and Ogana, Saitama Prefecture (KANNO, 1960: 370-371) and the lower part of the Aoki Formation

(lower Miocene) of Higashi-Kawate, Nagano Prefecture, Honshu (KURODA in HOMMA, 1931: 78; also see NELSON, 1974: 200-201). *Neptunea? (Golikovia?) ikusaensis* Krish-tofovich in Krish-tofovich and Ilyina, 1954 occurs in the upper part of the Takaradai Formation on the Kril'on Peninsula and the lowermost part of the Machigar Formation (both upper Oligocene) along the Ikusa River in southern Sakhalin (*ibid.*, 108). Thus, *N. (Golikovia)* and *N. (Neptunea)* were distinct taxonomically by the late Oligocene (Figure 14). Buccinaceans identified as *Neptunea* from the coeval Il'khatun Formation on Karagin Island (GLADENKOV, 1972: 141-142) (Figure 1) have been reassigned to *Trominina* (Gladenkov, *in litt.*, June 28, 1976).

Populations of *Neptunea (Golikovia)* sp. reached southeastern Kamchatka (SALIN, 1972: 62; table 3; Ust' Kamchatsk Formation) during the early Miocene. Species of *N. (Sulcosipho)* and *N. (Neptunea)* occur in the latest early Miocene faunas in northern Sakhalin. Definite *Neptunea*, representing the three recognized subgenera and two of the four stocks of *N. (Neptunea)*, first appear in large numbers in most of the (provincial) earliest middle Miocene molluscan faunas of Honshu, Hokkaido, Sakhalin, the Kuril Islands, Kamchatka, Karagin Island, the Alaska Peninsula (rare), Kodiak Island (rare), and southeastern

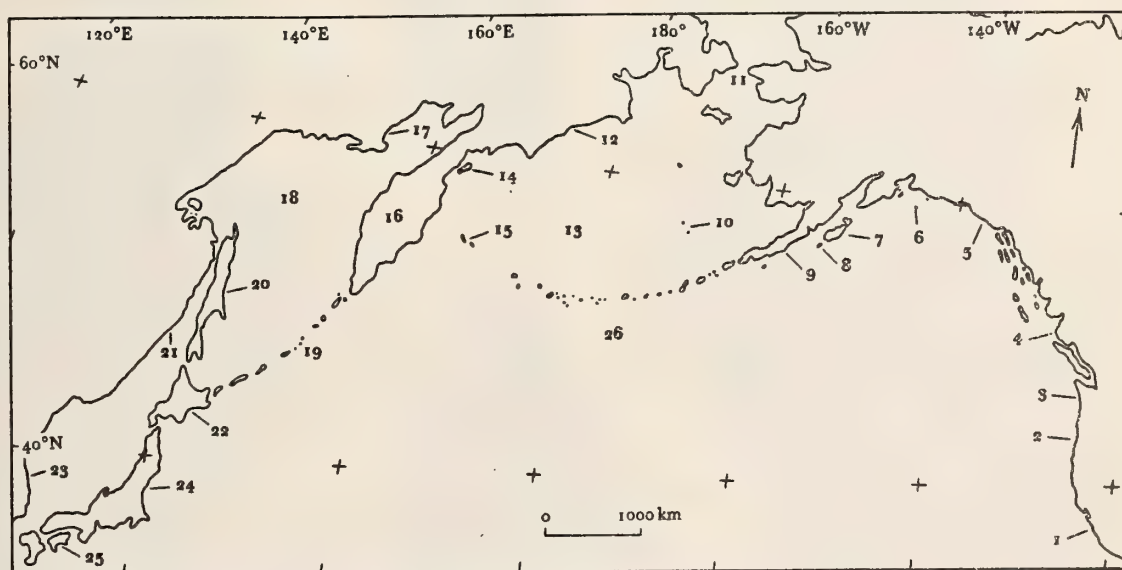


Figure 1

Localities cited in the text: (1) California; (2) Oregon; (3) Washington; (4) British Columbia, Canada; (5) southeast Alaska; (6) Middleton Island; (7) Kodiak Island; (8) Tugidak Island; (9) Alaska Peninsula; (10) Pribilof Islands; (11) Bering Strait; (12) Koryak coast; (13) Bering Sea; (14) Karagin

Island; (15) Komandor Islands; (16) Kamchatka; (17) Kolym coast; (18) Sea of Okhotsk; (19) Kuril Islands; (20) Sakhalin; (21) Primorye coast; (22) Hokkaido; (23) Korea Peninsula; (24) Honshu; (25) Shikoku; (26) North Pacific Ocean

Alaska. In the eastern portion of the Gulf of Alaska Tertiary Province, they are associated with cooler-water mollusks including the giant pectinid *Patinopecten* (*Lituyapecten*) (MACNEIL, 1961: 228; KANNO, 1971: 52-55; ADDICOTT, 1974: 191) and the neptuneid *Beringius*. There, *Neptunea* may have replaced ecologically *Liracassis*, or perhaps *Eosiphonalia*, of the warmer-water Oligocene and Miocene faunas. In subsequent Neogene *Neptunea*, especially within the nominate subgenus, taxonomic diversity is consistently greater in the western North Pacific (compare Figures 20 and 21), where it reaches a maximum in the Hokkaido-Sakhalin region during the late Miocene and early Pliocene. The eastern North Pacific acme occurred during the late Pliocene in the Alaska region.

ZOOGEOGRAPHIC REGIONS

The numerous depositional basins of the Neogene of the North Pacific margin and adjacent Bering Sea have been placed within six geographic regions. In this way, provincialism in stage-age unit terminology can be avoided while viewing the trends in zoogeography and taxonomic diversity within *Neptunea*. The western regions include those of Shikoku-Honshu (33°-42° N, including northern Kyushu and the Korea Peninsula), Hokkaido-Sakhalin (42°-55° N, including Primorye and the southern and central Kurils), and Kamchatka (50°-60° N, 155°-170° E., including the northern Kurils, Komandor Islands, Karagin Island, and the Kolym and Koryak coasts). California (30°-39° N), Oregon-Canada (39°-54° N), and Alaska (54°-60° N, 130°-180° W) comprise the eastern regions. The eastern regions are equivalent in part to those used in ADDICOTT's (1974: 188; text fig. 5) analysis of giant pectinids. In the zoogeographic charts (Figures 16-19), small circles represent the nearest occurrences in time and space of species in the same subgenera or stocks in the opposite half of the North Pacific.

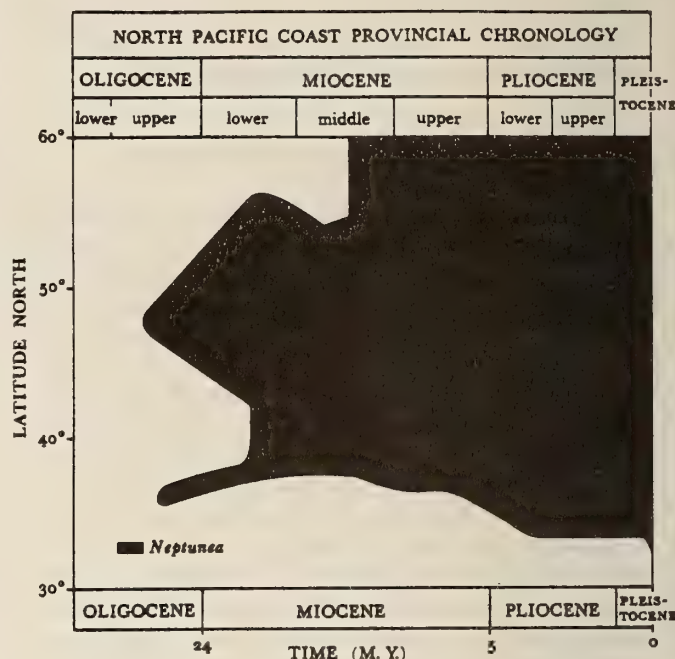


Figure 14

Zoogeographic and chronostratigraphic distribution of *Neptunea* in the North Pacific and adjacent Bering Sea during the late Cenozoic.

GEOCHRONOLOGY

The ages assigned to the boundaries of the Neogene chronostratigraphic units in the eastern North Pacific conform to those used by ADDICOTT (1976: text fig. 1; 1977: text fig. 3). They are based on the international standard of BERGGREN (1972) and BERGGREN & VAN COUVERING (1974).

Explanation of Figures 8 to 13

(all Figures × 1)

Figure 8: *Neptunea* (*Neptunea*) *lyrata altispira* (Gabb). USNM 250503. USGS Cenozoic loc. M1741. Yakataga Formation, lower Pleistocene part. Middleton Island, Alaska.

Figure 9: *Neptunea* (*Neptunea*) *pribiloffensis pribiloffensis* (Dall). USNM 250504. USGS Cenozoic loc. M3966. Elk River Formation, lower Pleistocene. Curry County, Oregon.

Figure 10: *Neptunea* (*Golikovia*) *smirnia* (Dall). USNM 250505. USGS Cenozoic loc. M2106. Capistrano Formation, lower Pliocene part. Orange County, California.

Figure 11: *Neptunea* (*Sulcosipho*) *lawsoni* (Martin). CAS Geology 59073. CAS Geology loc. 117. Rio Dell Formation, upper Pliocene. Humboldt County, California.

Figure 12: *Neptunea* (*Sulcosipho*) sp. B. aff. *N. (S.) tabulata* (W. Baird). USNM 250506. USGS Cenozoic loc. M1882. Yakataga Formation, lower Pliocene part. Karr Hills, Malaspina district, Alaska.

Figure 13: *Neptunea* (*Sulcosipho*) *tabulata* (W. Baird). USNM 250507. USGS Cenozoic loc. M2753. Fernando Formation, upper Pliocene part. Orange County, California.



Figure 8



Figure 9



Figure 10



Figure 11

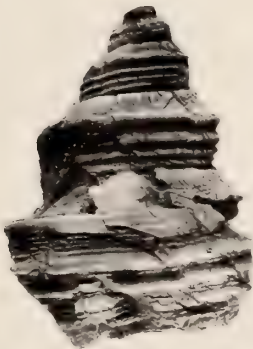


Figure 12



Figure 13

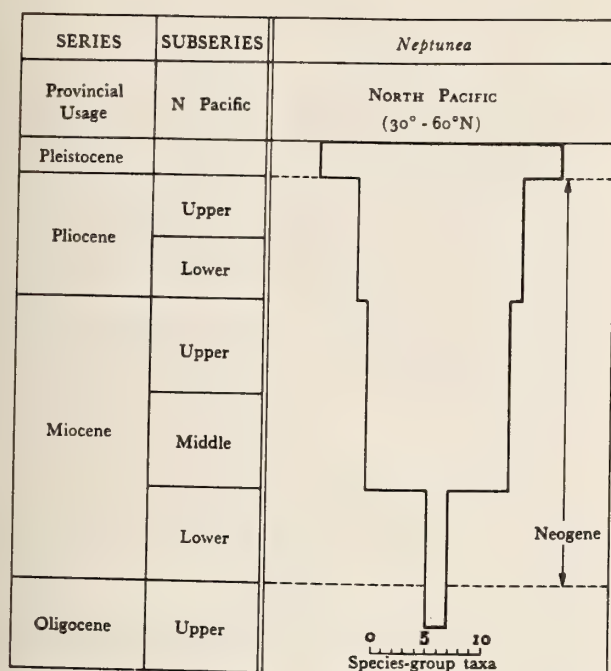


Figure 15

Chronostratigraphic occurrence and taxonomic diversity of *Neptunea* in the North Pacific and adjacent Bering Sea during the late Cenozoic.

Provincial stage-age units for the Neogene molluscan sequences in southern Alaska have not been established as yet, although ALLISON (1977a: text fig. 1; 1977b: 876) correlated the mollusk-bearing formations of the Gulf of Alaska with Addicott's chronostratigraphic units. In the western North Pacific, subseries-subepoch units based principally on the chronostratigraphic framework of GLADENKOV (1972, 1974) are used in displaying trends in taxonomic diversity and zoogeography within *Neptunea*.

Neptunea (*Sulcosipho*)

MORPHOLOGY

Medium to large, slender elongate-fusiform shells, with tabulate to subtabulate or rounded whorl shoulders and subsulcate to channeled subsutural shelves distinguish taxa in *Neptunea* (*Sulcosipho*). For all of the subgenera, the lengths of adult shells have been classed as: "small," 50-75

mm; "medium," 75-125 mm; "large," 125-175 mm; and "very large," more than 175 mm. The notation of the primary spiral ribs on the first adult whorl is $(A_{1a_1})B_1C_1(D_1)$; B is at a position posterior to the middle of the spire whorls. The B, C, and D ribs, rounded to subcrenulate in cross-section and often bifurcated by narrow grooves, are developed strongly on the initial adult whorls and separated by narrower interspaces. Secondary spiral ribs fill each interspace on second and third adult whorls. Tertiary spirals, inserted anteriorly, alternate regularly with the stronger elements. Shell morphology in *N. (Sulcosipho)* is more similar to that of *N. (Neptunea)* than to *N. (Golikovia)*.

ZOOGEOGRAPHY AND TAXONOMIC DIVERSITY

Taxa in *Neptunea* (*Sulcosipho*) were distributed circum-boreally in the North Pacific during the middle and late Miocene. Specimens of *N. (S.) "sachalinensis"* Khomenko, 1938, from the Kaskadn (upper lower Miocene) and Vengeri (middle Miocene) Formations on the Shmidt Peninsula of northern Sakhalin, represent the earliest occurrence of *N. (Sulcosipho)* in the western North Pacific. Species of the subgenus occur throughout the western North Pacific during the late Miocene (Figure 16). They occur only in the Shikoku-Honshu region during the Pliocene, where maximum taxonomic diversity in the Neogene of the western North Pacific is reached early in the epoch (Figure 20). *Neptunea (S.) lamellosa* Golikov, 1962, occupied northern portions of the Sea of Okhotsk in the Pleistocene.

An unnamed species (Figure 12) of *Neptunea (Sulcosipho)*, ancestral to *N. (S.) tabulata* (W. Baird, 1863) (Figure 13) from the lower part of the Yakataga Formation (lower middle Miocene part) in the Yakataga district of the Gulf of Alaska Tertiary Province, represents the earliest known occurrence of *N. (Sulcosipho)* in the eastern North Pacific (Figure 17). Subsequent populations of this species and a closely-related new species occurred as far north as Middleton Island (Figure 1) in the Gulf of Alaska through the early Pleistocene. Other species extended their ranges southward to the Canada-Oregon region during the early Pliocene, where maximum taxonomic diversity within *N. (Sulcosipho)* occurred late in the epoch (Figure 21). They reached the California region in the late Pliocene and Pleistocene. This trend parallels the inferred progressive cooling of inshore waters during the Pliocene (DURHAM, 1950; ADDICOTT, 1969, 1974). *Neptunea (S.) andersoni* (Martin, 1914), restricted to the early Pliocene of the southernmost portion of the Oregon-Canada region, evolved from emigrants of the *N. (S.) uwasoensis* (Otuka, 1935) lineage of the western North Pacific.

Neptunea (Golikovia)

MORPHOLOGY

HABE & SATO (1972: 2, 6) proposed *Neptunea* (Golikovia) as a full genus, but the radular morphology and number they thought to be unique also occur in two species of *N.* (*Neptunea*) (see GOLIKOV, 1963: 29, 75). Thus, separate generic status for *Golikovia* is not appropriate. The notation and configuration of primary spiral ribs indicate that *N.* (Golikovia) is more closely related to *Neptunea* than to any other neptunoid genus.

Species of *Neptunea* (Golikovia) exhibit medium to very large, subelongate-fusiform shells, with slender to moderately inflated, convex whorls that have rounded, non-tabulate shoulders (Figure 10). Seven or eight unique, equal-sized, rounded to subcrenulate primary spiral ribs on posterior adult whorls distinguish the subgenus. Their notation is $(A_1, a_1)B_1C_1D_1E_1(F_1)(G_1)(H_1)$; B is located near the posterior suture of the spire whorls. These spiral ribs are separated on posterior whorls by interspaces equal to or slightly wider than the ribs. Subordinate ribs are reduced and all spiral sculpture usually weakens to obsolescence anteriorly on the penultimate and body whorls.

ZOOGEOGRAPHY AND TAXONOMIC DIVERSITY

Taxa in *Neptunea* (Golikovia) were distributed circum-boreally in the North Pacific during the middle Miocene. Following uncertain records from upper Oligocene strata on Sakhalin (KRISHTOFOVICH in KRISHTOFOVICH & ILYINA, 1954) and lower Miocene strata on Kamchatka (SALIN, 1972), the next known occurrence of the subgenus in the western North Pacific is *N.* (G.) *nikkoensis* (non) Nomura, 1937 (NODA, 1962) from the Kubiki Formation (middle Miocene) of Tanaoka, Niigata Prefecture, Honshu. Species of *N.* (Golikovia) migrated to the southern portion of the Shikoku-Honshu region in the late Miocene. Their distribution was restricted to the Hokkaido-Sakhalin and Shikoku-Honshu regions during the Pliocene, and to the latter region alone in the Pleistocene, where *N.* (G.) *fukuae* Kira, 1959 represented the subgenus. Southern populations of this species apparently extended their range in the submerged Oyashio water mass southwestward to Shikoku during the late Pleistocene and Holocene (Figure 16).

The earliest species of *Neptunea* (Golikovia) from the eastern North Pacific is *N.* (G.) *plafkeri* Kanno, 1971 from the lower part of the Yakataga Formation in the Yakataga

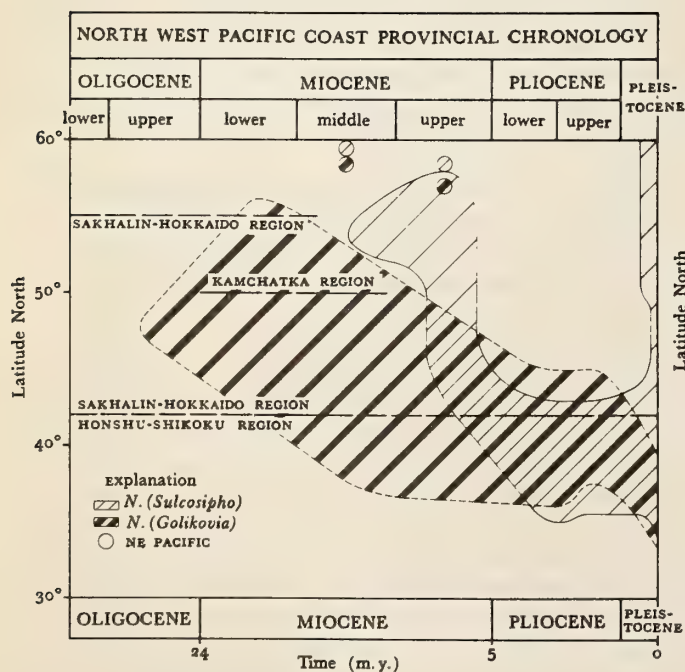


Figure 16

Zoogeographic and chronostratigraphic distribution of *Neptunea* (*Sulcosipho*) and *Neptunea* (*Golikovia*) in the western North Pacific and adjacent Bering Sea during the late Cenozoic.

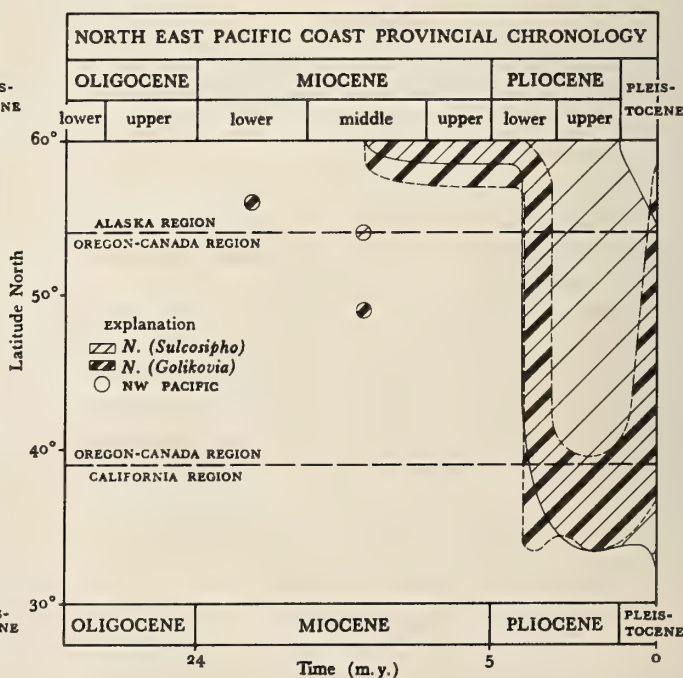


Figure 17

Zoogeographic and chronostratigraphic distribution of *Neptunea* (*Sulcosipho*) and *Neptunea* (*Golikovia*) in the eastern North Pacific and adjacent Bering Sea during the late Cenozoic.

district and the Topsy Formation (both Miocene) in the Lituya district of southeastern Alaska (Figure 17). In the early Pliocene, *N. (Golikovia)* expanded rapidly southward to California. Its species were restricted to the southern Oregon-Canada and California regions during the late Pliocene. Maximum taxonomic diversity within the subgenus in the Neogene of the eastern North Pacific occurred in the California region during the late Pliocene (Figure 21). *Neptunea (G.) phoenicea* (Dall, 1891), whose modern distribution extends as far north as Juneau, Alaska, may have evolved from a western North Pacific lineage in the early Pliocene. Both *N. (Golikovia)* and *N. (Sulcosipho)* display lesser species diversity in the Neogene compared to that of *N. (Neptunea)* (compare Figures 20 and 21).

Neptunea (Neptunea)

Small to very large, subfusiform to fusiform shells, with shortened to sub-elongate spires and angular subtabulate to rounded convex whorls distinguish species of *Neptunea (Neptunea)*. They have reduced penultimate whorls and moderately to greatly inflated body whorls compared to shells of the other subgenera. Subsutural shelves are sloped gently and not subsulcate or channeled on anterior whorls. The notation of the initial spiral sculpture varies, but usually contains well-developed B and C primary ribs; B is located at, or just anterior to, the middle of the spire whorls. The notation and configuration of spiral ribs define four stocks of closely-related species lineages within *N. (Neptunea)*: *N. (N.) lyrata* (Gmelin, 1791), *N. (N.) pribiloffensis* (Dall, 1919), *N. (N.) despecta* (Linnaeus, 1758), and *N. (N.) eulimata* (Dall, 1907).

Neptunea (Neptunea) eulimata (Dall) Stock

Species in the *N. (N.) eulimata* (Dall) stock are characterized by large to very large, elongate-fusiform shells with shallow to inflated convex or rounded subtabular whorls. Often the spire or all whorls are especially slender. Very thin, shallowly to moderately-rounded convex primary ribs, with the notation (A_1, a_1) $B_1C_1D_1$, increase in width anteriorly to a maximum of one millimeter. Interspaces between the B and C ribs vary in width to twice that of the ribs. Single secondaries are inserted early on posterior whorls; spacing and number of secondary and tertiary elements become irregular anteriorly. These shells often bear thin to medium-sized, widely-spaced axial lobes or lamellae. The stock is endemic to the western North Pacific and is represented initially by *N. (N.) iwaii* Hatai, Masuda, and Suzuki, 1961 from the Hamada Formation (lower Pliocene) and coeval units in Aomori Prefecture, northern

Honshu. From this species evolved the two Holocene species of the northern portion of the Shikoku-Honshu region and southern part of the Hokkaido-Sakhalin region (Figure 18).

Neptunea (Neptunea) lyrata (Gmelin) Stock

MORPHOLOGY

In the *N. (N.) lyrata* (Gmelin) stock, the notation of the initial sculpture is (a_1) $B_1(C_1, c_1)(D_1, d_1)$. The B spiral rib, located usually at the maximum diameter of the spire whorls, is stronger than the C or D ribs when the latter pair are present. These rounded and protuberant spirals enlarge anteriorly to widths of more than two millimeters. Interspaces between the B and C primaries on the spire whorls are narrower than the ribs. Secondary and tertiary spiral elements are less well-developed than those of species in the other stocks.

ZOOGEOGRAPHY AND TAXONOMIC DIVERSITY

The *Neptunea (N.) lyrata* (Gmelin) stock was distributed circumboreally in the North Pacific during the middle and late Miocene; it has occupied the continental shelf and uppermost slope in the Bering Sea since at least the late Pliocene. The earliest known species of the stock in the western North Pacific is represented by specimens of *N. (N.) "sachalinensis"* Khomenko, 1938, from the upper Kasakadn (upper lower Miocene) and lower Vengeri (lower middle Miocene) Formations on the northwestern Shmidt Peninsula of Sakhalin. *Neptunea (N.) pluricostulata* Ilyina, 1939 (Figure 2) and *N. (N.) unicostulata* Ilyina, 1939 (Figure 3) occur in the middle Miocene strata of Sakhalin and Kamchatka (ILYINA, 1939, 1954, 1963; GLADENKOV, 1972). Subsequently, species of this stock were distributed widely in all three regions of the western North Pacific from the late Miocene through the Pleistocene (Figure 18); they attained their maximum taxonomic diversity in the Neogene during the early Pliocene (Figure 20).

In the eastern North Pacific, the *Neptunea (N.) lyrata* (Gmelin) stock is represented initially by an unnamed species of the arcto-boreal *N. (N.) heros* (Gray, 1850) lineage. It and *N. (N.) pluricostulata* Ilyina, from the western North Pacific, occur in the lower part of the Yakataga Formation (lower middle Miocene part) of the Katalla and Yakataga districts in southeastern Alaska (Figure 19). The widely distributed *N. (N.) lyrata altispira* (Gabb, 1869) (Figures 6-8) evolved from the latter species in the Gulf of Alaska during the latest middle or earliest late Miocene. The *N. (N.) lyrata* stock was confined to the Alaska region

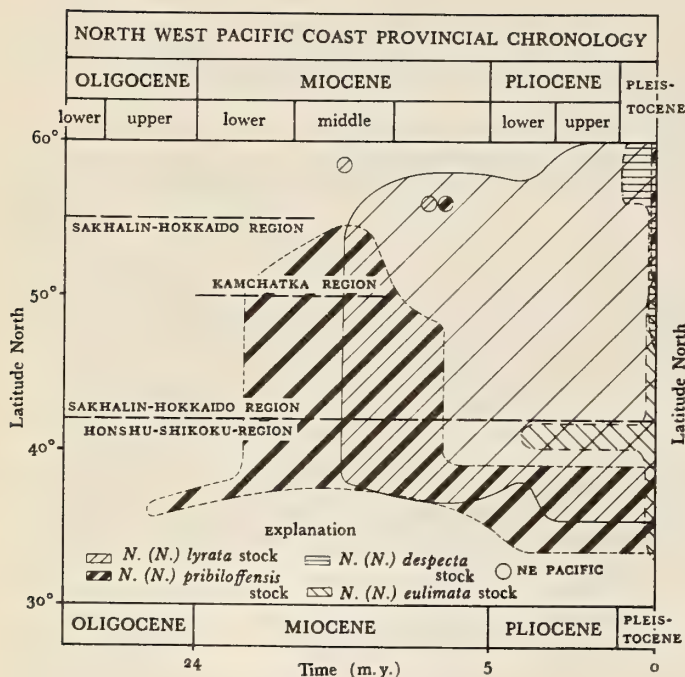


Figure 18

Zoogeographic and chronostratigraphic distribution of *Neptunea* (*Neptunea*) stocks in the western North Pacific and adjacent Bering Sea during the late Cenozoic.

during the Miocene and early Pliocene and expanded southward to the Canada-Oregon region in the late Pliocene and Pleistocene, the interval of its maximum taxonomic diversity in the eastern North Pacific (Figure 21). Despite numerous literature citations to the contrary, species of this stock do not occur in the Neogene or Quaternary of the California region.

Neptunea (*Neptunea*) *pribiloffensis* (Dall) Stock

MORPHOLOGY

The general notation of the spiral ribs on shells of species in the *Neptunea* (*N.*) *pribiloffensis* (Dall) stock is $(a_1)B_1C_1(D_1)$. These shells exhibit rounded convex B, C, and D ribs, which are nearly of equal size on posterior whorls. On anterior whorls, the ribs are usually less than two mm in width. The C rib is located at the maximum diameter of the whorls. Interspaces between the B and C ribs on middle and anterior whorls are broader than the

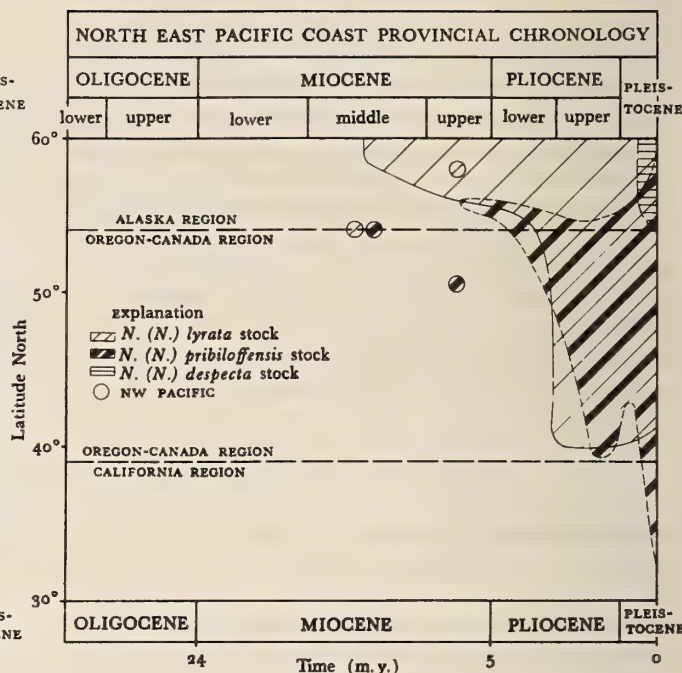


Figure 19

Zoogeographic and chronostratigraphic distribution of *Neptunea* (*Neptunea*) stocks in the eastern North Pacific and adjacent Bering Sea during the late Cenozoic.

ribs. Strong, single secondary and multiple tertiary spirals are developed more prominently on these shells than those of the *N. (N.) lyrata* (Gmelin) stock.

ZOOGEOGRAPHY AND TAXONOMIC DIVERSITY

Members of the *Neptunea* (*N.*) *pribiloffensis* (Dall) stock were distributed circumboreally in the North Pacific during the late Miocene. They have occupied the continental shelf and uppermost slope in the Bering Sea since at least the late Pliocene. The known fossil record of this stock does not support STRAUCH's (1972: text fig. 2) suggestion that *N. (N.) pribiloffensis* (Dall) originated in the North Atlantic. The record of this species and its stock is confined to the North Pacific and southern Bering Sea.

Four distinct lineages evolved from Oligocene and Miocene populations of *Neptunea* (*N.*) *modesta* (Kuroda in Homma). This species occurs initially in the Nenokami Sandstone (upper Oligocene) of Chigaya and the Iwadonozawa, Saitama Prefecture (KANNO, 1960: 370) and the

lower part of the Aoki Formation (lower Miocene) of Kashiwa-zawa, northern Nagano Prefecture, Honshu (KURODA in HOMMA, 1931: 78 and explanation pl. 13). Species in these lineages occur in early Miocene faunas of the Shikoku-Honshu and Hokkaido-Sakhalin regions and in all three regions of the western North Pacific during the middle and late Miocene (Figure 18). Text citations report *N. (N.) pribiloffensis* (Dall) and related species from the lower part of the Enemten Formation (lower Pliocene) of central-western Kamchatka (SINEL'NIKOVA, 1969: 34; SINEL'NIKOVA & DRUSHCHITS, 1971: text fig. 2), where it occurs with *Fortipecten kenyoshiensis* (Chinzei), and in approximately coeval strata near Rekinniki and Pleistocene units elsewhere in northern Kamchatka (GOLIKOV, 1963: 150-151; text fig. 91). If verified, these would demonstrate a continuous record of the stock in the northern Hokkaido-Sakhalin and Kamchatka regions from the middle Miocene through the Pleistocene; as a related species occurs in the Mayamraf Formation (middle to upper Miocene) on the Shmidt Peninsula (KHOMENKO, 1934: 69) and in the lower part of the Maruyam I Formation (upper Miocene) along the Liutoga River in southern Sakhalin (ILYINA in KRISHTOFOVICH & ILYINA, 1954: 244). *Neptunea (N.) pribiloffensis* (Dall) also may have spread into the eastern portion of the Kamchatka region from the eastern Bering Sea during the Pleistocene. A geographical restriction of the stock's southern taxa began in the Pliocene. The Pliocene and Pleistocene *N. (N.) frater frater* (Pilsbry, 1901) and *N. (N.) frater "kuroshio"* Oyama, 1958 occur only in the Shikoku-Honshu region.

In the Neogene of the eastern North Pacific, the stock is consistently much less diverse taxonomically (peak: late Pliocene) than in the western North Pacific (peak: late Miocene) (compare Figures 20 and 21). *Neptunea (N.) modesta* (Kuroda in Homma) from the Bear Lake Formation (upper Miocene) near Port Moller on the Alaska Peninsula represents the earliest known occurrence of the stock in the eastern North Pacific. A closely-related, new species occurs in the lower part of the Tachilni Formation (upper Miocene to lower Pliocene) south of Fort Randall, Alaska Peninsula. *Neptunea (N.) pribiloffensis* (Dall) (Figure 9) occurs initially in the Tugidak Formation (upper Pliocene and lower Pleistocene) on Tugidak Island, Alaska (Figure 1) and questionably in the Rio Dell Formation (upper Pliocene) in northern California. This species originated from, or shared a common ancestry with, *N. (N.) "gigantea"* (KHOMENKO, 1934) and a closely-related, unnamed species from middle and upper Miocene strata on Sakhalin and lower Pliocene sediments on Kamchatka. The stock was distributed widely in the eastern North Pacific during the Pleistocene (Figure 19).

Neptunea (Neptunea) despecta (Linnaeus) Stock

MORPHOLOGY

Species in this stock are distinguished by primary spiral ribs which are rounded convex, subrounded, or triangular in cross-section and have the notation $(a_1)B_1C_1(d_1)$. The primary ribs attain widths of less than 2 mm on anterior whorls. The interspace between the B and C ribs is broader than the ribs on the middle and anterior whorls. Secondary and tertiary spiral elements are developed strongly on anterior whorls. Nodes or tubercles occur often on the primary and some secondary ribs of anterior whorls. Occasionally these whorls bear varices and lamellae of low-relief.

ZOOGEOGRAPHY

Although no species of this stock is known from the Neogene deposits of the North Pacific or Bering Sea, *Neptunea (N.) borealis* (Philippi, 1850) (Figure 4) occurs in the Olkhov Formation (lower Pleistocene) of the Tusatuvayam [Anvilian] Transgression near Ust' Kamchatsk, Kamchatka and on Karagin Island (PETROV & KHOREVA, 1968; Petrov, unpublished data; NELSON, 1974: 258-259) (Figure 18). This species occupied most of the continental shelf in the Bering Sea during the Pleistocene. In the eastern Bering Sea, it occurs initially in middle Pleistocene strata of the Einahnuhtan Transgression on St. Paul Island in the Pribilofs (D. M. Hopkins, unpublished data; NELSON, 1974: 258) (Figure 19).

Neptunea in the Arctic and North Atlantic

During the late Pliocene Beringian Transgression, *Neptunea* species formed part of the spectacular dispersal of Pacific, or Pacific-related, boreal mollusks through Bering Strait, across the Arctic, and into the North Atlantic (MACNEIL, 1957: 113; 1965: 68-69; GOLIKOV, 1963: 51-53; fig. 60; DURHAM & MACNEIL, 1967: 336; HOPKINS, 1967: 59; 1972: 124-125; STRAUCH, 1972: text fig. 2; MACNEIL, 1973: 56; NELSON, 1973: 85). Species in *N. (Sulcosipho)* and the *N. (N.) lyrata* (Gmelin) and *N. (N.) despecta* (Linnaeus) stocks occupied the Pliocene and Pleistocene basins of Iceland and the North Sea; those of *N. (Sulcosipho)* expanded into the western Mediterranean during the Pleistocene (NELSON, 1973: 85; 1974: 52-57; 1977: 375-376). The known record of *Neptunea* in the western North Atlantic dates from the late Pleistocene, when it extended as far south as New Jersey. Modern *Neptunea* occur over nearly the entire continental shelf of the Arctic Ocean, north of

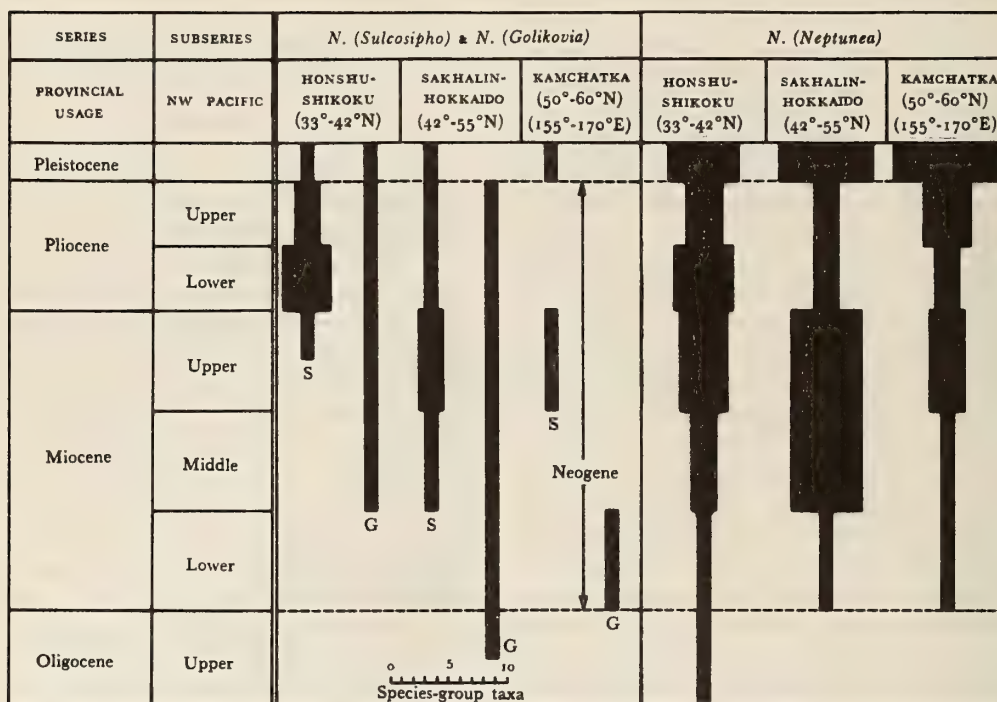


Figure 20

Chronostratigraphic occurrence and taxonomic diversity of western North Pacific and adjacent Bering Sea during the late Cenozoic.

Neptunea (Sulcosipho), *N. (Golikovia)*, and *N. (Neptunea)* in the

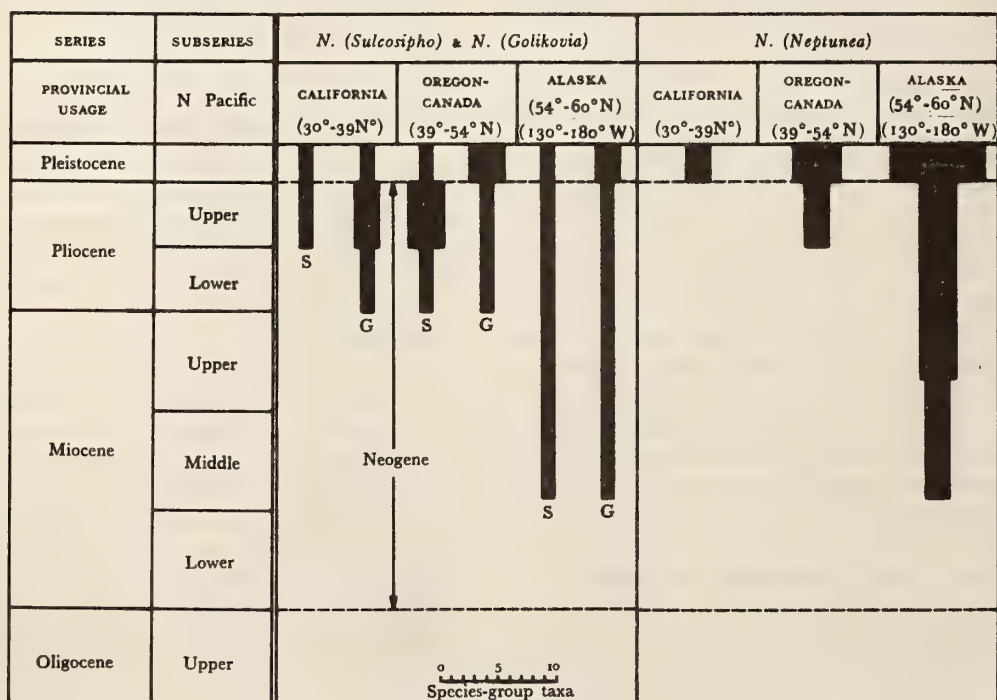


Figure 21

Chronostratigraphic occurrence and taxonomic diversity of eastern North Pacific and adjacent Bering Sea during the late Cenozoic.

Neptunea (Sulcosipho), *N. (Golikovia)*, and *N. (Neptunea)* in the

Martha's Vineyard, Massachusetts, in the western North Atlantic, and north of Cape Spartel, Morocco, in the eastern North Atlantic (NELSON, 1974).

SUMMARY

Neptunea evolved in waters off northern Japan and Sakhalin during the early Oligocene from taxa sharing a common ancestry with *Ancistrolepis altispirata* (Nagao). Thus it is a more "modern" taxon than portrayed previously. *Neptunea* species spread north and east during the late Oligocene and early Miocene. By the early middle Miocene, *Neptunea* occupied the rim of the North Pacific and adjacent Bering Sea from Honshu to southeastern Alaska. Regions south of Alaska were peripheral to the major evolutionary center of the genus in the Neogene and Quaternary. Several species occurred south of Alaska beginning in the Pliocene. Taxonomic diversity increased significantly during the middle Miocene and reached somewhat higher levels during the Pliocene. Species of *N. (Neptunea)* were distributed widely during that interval. Those of the other subgenera were more conservative, both in their evolution and geographic distribution; they were restricted to latitudes south of Alaska after the Pliocene. Taxonomic diversity within *N. (Neptunea)* increased even more during the latest Pliocene and Pleistocene, as the genus expanded into the Arctic, North Atlantic, and the western Mediterranean.

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was a Research Fellow in the Museum of Paleontology at the University of California, Berkeley, during 1975-1976.

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- M1741. Cliff near SW end of Middleton Island, Middleton Island B-7 quad. (1 : 63 360, 1955), Alaska. Yakataga Formation, about 1013 m above base of 1181 m exposed section, as determined by PLAFKER (1971: 129), lower Pleistocene part
- M1882. Karr Hills, at 60°08'N, 148°19'W, Bering Glacier quad. (1 : 250 000, 1959), Malaspina district, Alaska. Yakataga Formation, from interval above 975 m above base of 2130 m Yakataga exposed section, lower Pliocene part
- M2106. In artificial cut, elevation about 149.4 m, on N side of Deep Canyon, 1342 m S and 731 m W of NE corner [projected] Sec. 13, T.8 S., R. 8 W., Dana Point quad. (7.5 min., 1 : 24 000, 1949), Orange County, California. Uppermost part of Capistrano Formation, lower Pliocene
- M2753. In artificial cut near top of bluff overlooking Upper Newport Bay, elevation about 27.4 m, approximately 837.5 m SE and 776.6 m SW from N corner Irvine Block 52, Newport Beach quad. (7.5 min., 1 : 24 000, 1965), Fernando Formation, lower part of upper unit, upper Pliocene
- M3966. *Psephidia* beds exposed in slumped blocks SE of mouth of Elk River, 91.4 m S and 60.9 m E of NW corner of Sec. 18, T.32 S., R. 15 W., Cape Blanco quad. (15 min., 1 : 62 500, 1954), Curry County, Oregon. Elk River Formation, lower Pleistocene

University of California (Berkeley), Museum of Paleontology (UCMP):

- B7644. In E side of bed of Eel River, from 441.9 m to 472.4 m NE of U. S. Highway 101 bridge, in center of SE, SW, Sec. 5, T. 1 N., R. 1 E., Scotia quad. (15 min., 1 : 62 500, 1951). Humboldt County, California. Rio Dell Formation, massive dark gray sandy siltstone about 376.4 m above base, upper Pliocene (? = CAS loc. 117)
- B7879. Cliff, about 6.1 m E of railroad trestle and 141.7 m N of place where Nanning Creek passes under the railroad tracks, in center of NE, Sec. 5, T. 1 N., R. 1 E., Fortuna quad. (15 min., 1 : 62 500, 1942), Humboldt County, California. Rio Dell Formation, 143.3 m below top (1213.9 m above base), upper Pliocene
- D3712. Point Nepropusk, about 100 km N of Tichil' River, west coast of Kamchatka, U. S. S. R. Etolon Formation (Kavran Group), upper Miocene of GLADENKOV (1972)

California Academy of Sciences (CAS):

- 117. Along E bank of Eel River, 1.2 km N of Scotia, "Scotia Quad.," Humboldt County, California. Wildcat Group, probably lower part of Rio Dell Formation, upper Pliocene (collected in 1912; probably equivalent to UCMP loc. B7644)

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Late Neogene Succession of Molluscan Fauna on the Pacific Coast of Southwestern Japan, with Reference to Planktonic Faunal Sequence

BY

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Shizuoka University, Japan

(6 Text figures)

INTRODUCTION

THE PACIFIC COAST of southwestern Japan is dotted with late Neogene marine sediments in several areas, as seen in the Kakegawa district west of Shizuoka, the Tonohama district in south Shikoku, the Miyazaki district in east Kyushu, and the Okinawa and Miyako districts in the Southwestern Islands (Ryukyu Islands) (Figure 1).

Of these, the Kakegawa district is one of the type areas of the Japanese Neogene where deposits are extensive and continuous, consisting of early and late Neogene series. The late Neogene series, ranging in age from late Miocene to early Pleistocene, is composed of open coastal sediments, with frequent pyroclastic intercalations, some of which have been dated by the fission track method. Mollusks are especially abundant in coarse and shallow sediments in the north, that is, a paleogeographically nearshore area; however, rich planktonic foraminifera are contained in finer and deeper sediments to the south, that is, the offshore area at that time. Pyroclastic layers intercalated in the nearshore facies are useful for the chronostratigraphic subdivision. Biostratigraphically, the series has been divided into several stages by means of the molluscan faunal succession.

As a result of our recent field survey, some important pyroclastic layers were found to extend southward into the offshore facies. Paleomagnetic surveys have also been made. It is now possible, therefore, to correlate the molluscan faunal succession in the northern section with the planktonic foraminiferal sequence in the southern section. In this paper, the authors would like to demonstrate the interrelationship between molluscan stages and worldwide

planktonic foraminiferal zones in the late Neogene sections of the Kakegawa district.

GEOLOGY OF THE LATE NEOGENE SERIES

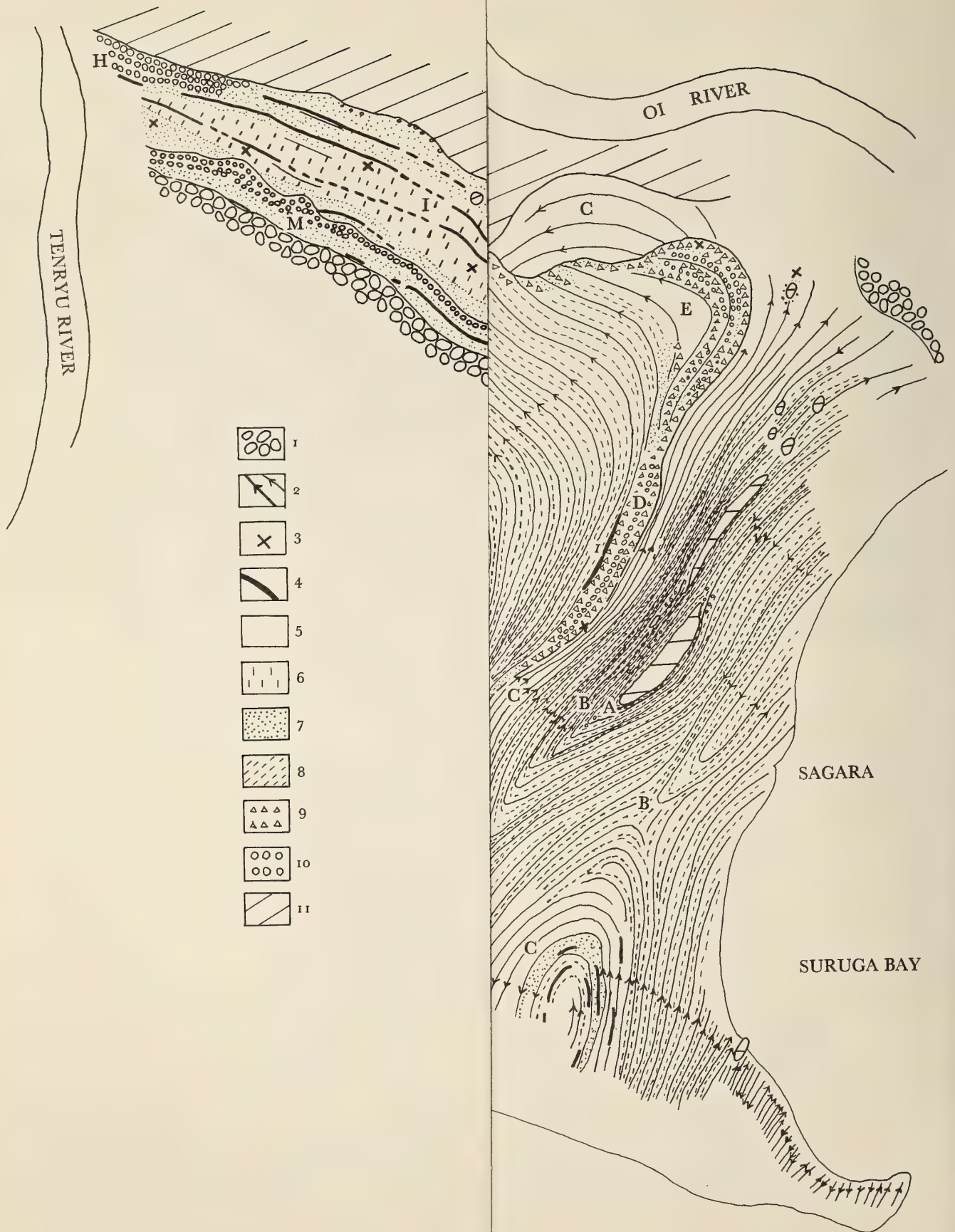
As the geology and stratigraphy of the late Neogene series in the Kakegawa district have already been elucidated (TSUCHI, 1961, 1969, 1976), an outline is given here. The



Figure 1

Distribution of late Neogene sediments on the Pacific coast of southwestern Japan, and index map of the Kakegawa district

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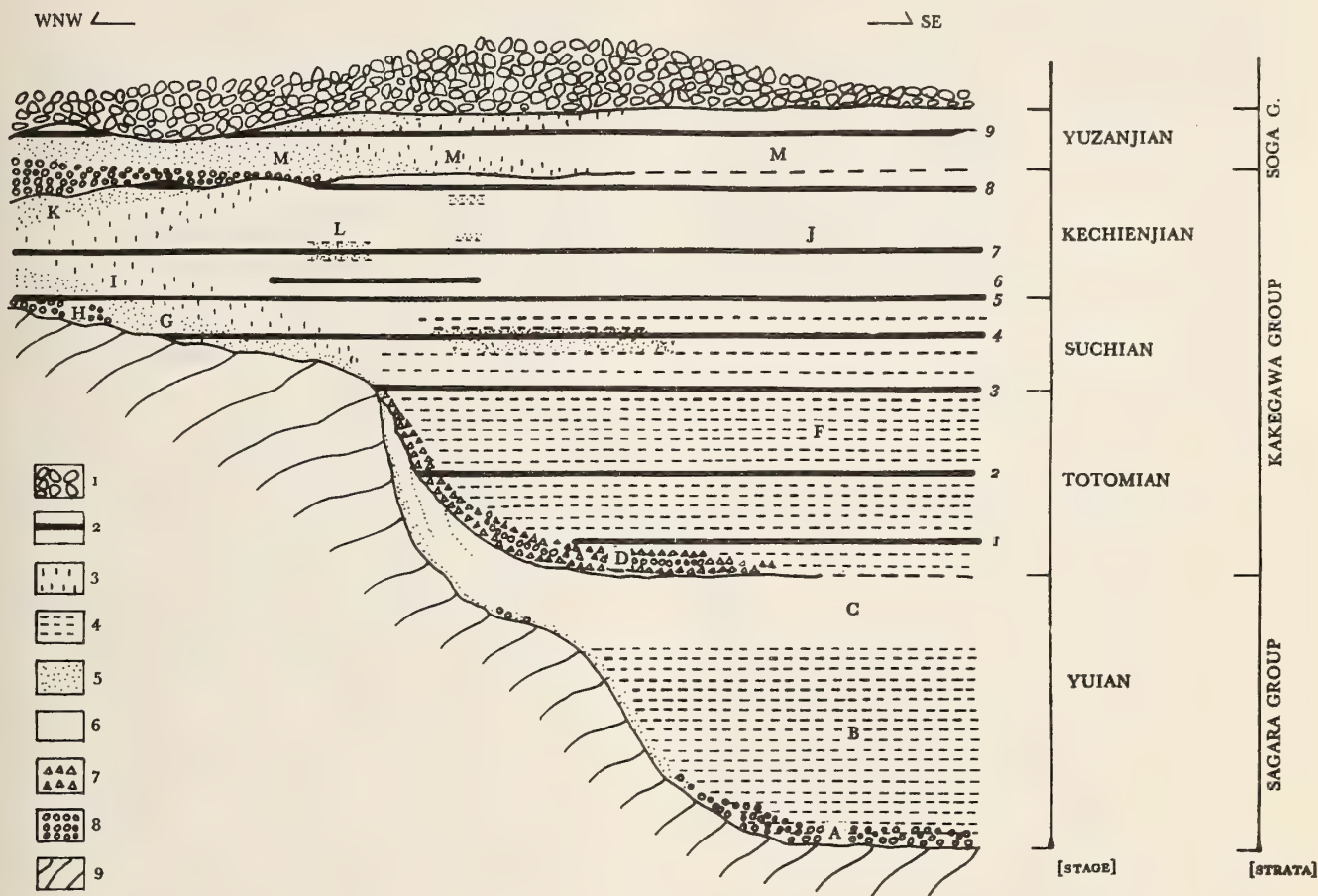


Figure 3

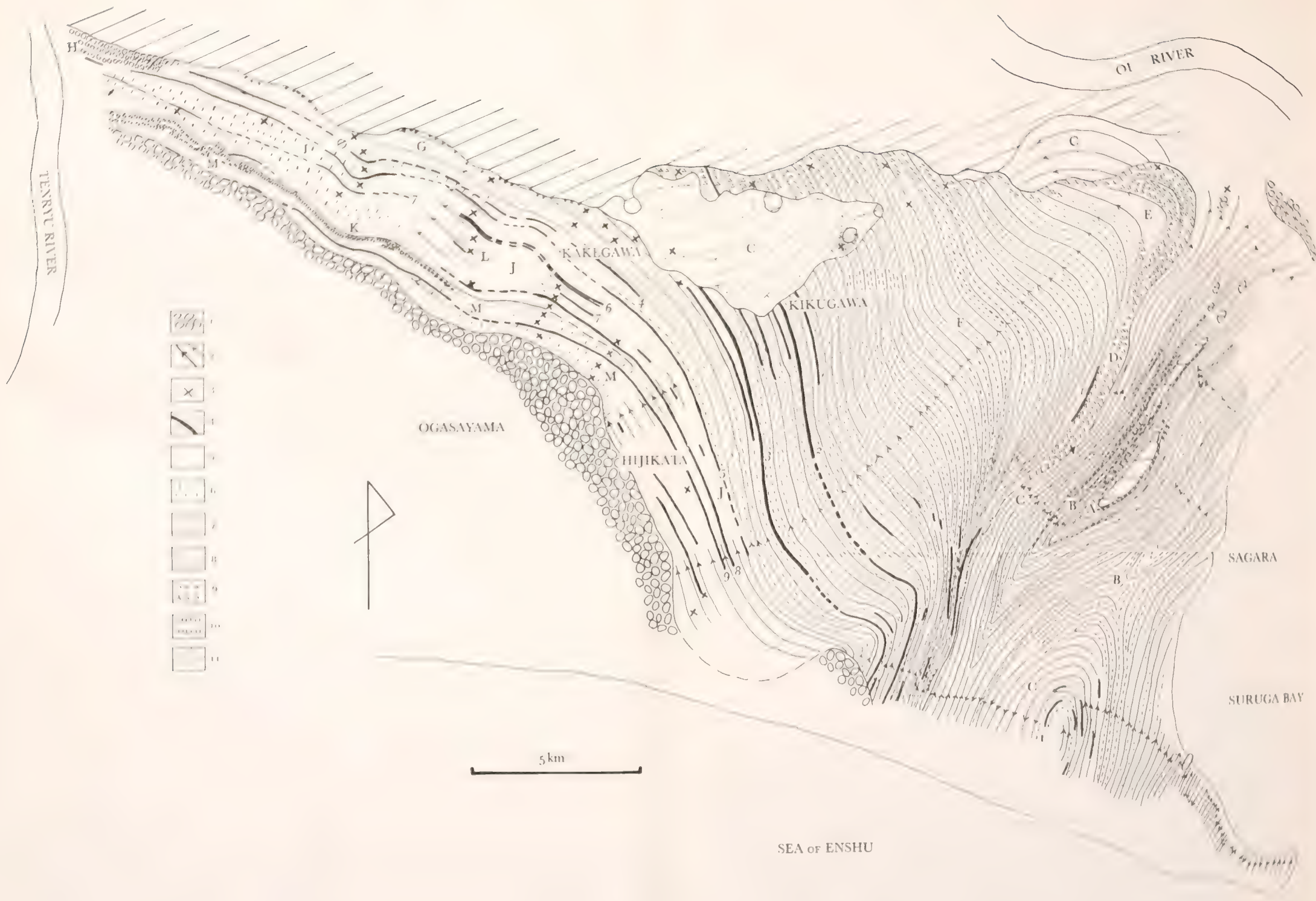
Idealized profile of the late Neogene series of the Kakegawa district
1: Pleistocene Ogasayama Gravels. 2: Pyroclastic layer. 3:

Silty sand. 4: Alternation of sand and silt. 5: Sand. 6: Silt.
7: Angular or subangular pebbles or boulders. 8: Rounded or
subrounded pebbles. 9: Early Neogene series and pre-Neogene
complex. — Symbols 1 to 9 and A to M as in Figure 2.

Figure 2 (see foldout)

Geological map of the late Neogene series of the Kakegawa district
The map shows the horizontal section so as to clarify the structure.
1: Pleistocene Ogasayama Gravels. 2: Lines are drawn in
every 100 m in thickness of the strata and parallel to the strike.
The dip is given always on the left hand by the arrow. 3: Ap-
proximate location and horizon of main fossil localities. 4: Pyro-
clastic layer. 5: Silt. 6: Silty sand. 7: Sand. 8: Alter-
nation of sand and silt. 9: Angular or subangular pebbles or
boulders. 10: Rounded or subrounded pebbles. 11: Early
Neogene series and pre-Neogene complex.

1: Arigaya Tuff. 2: Shiraiwa Tuff. 3: Iozumi Tuff.
4: Agehari Tuff. 5: Hosoya Tuff. 6: Nishi-Kakegawa Tuff.
7: Sakuragi Tuff. 8: Kogoshō Tuff. 9: Soga Tuff.
A: Tokigaya Alternation of Granules, Sand and Silt. B: Sagara
Alternation of Sand and Silt. C: Oyori and Tamari Silt.
D: Hagima Conglomerate. E: Kiriya Silt. F: Horinouchi
Alternation of Sand and Silt. G: Dainichi Sand. H: Nobe
Conglomerate. I: Tenno Silty Sand. J: Hijikta Silt. K: A-
burayama Sand. L: Tombe Sand-rich Alternation. M: Soga
Group (gravels, sand and silt).



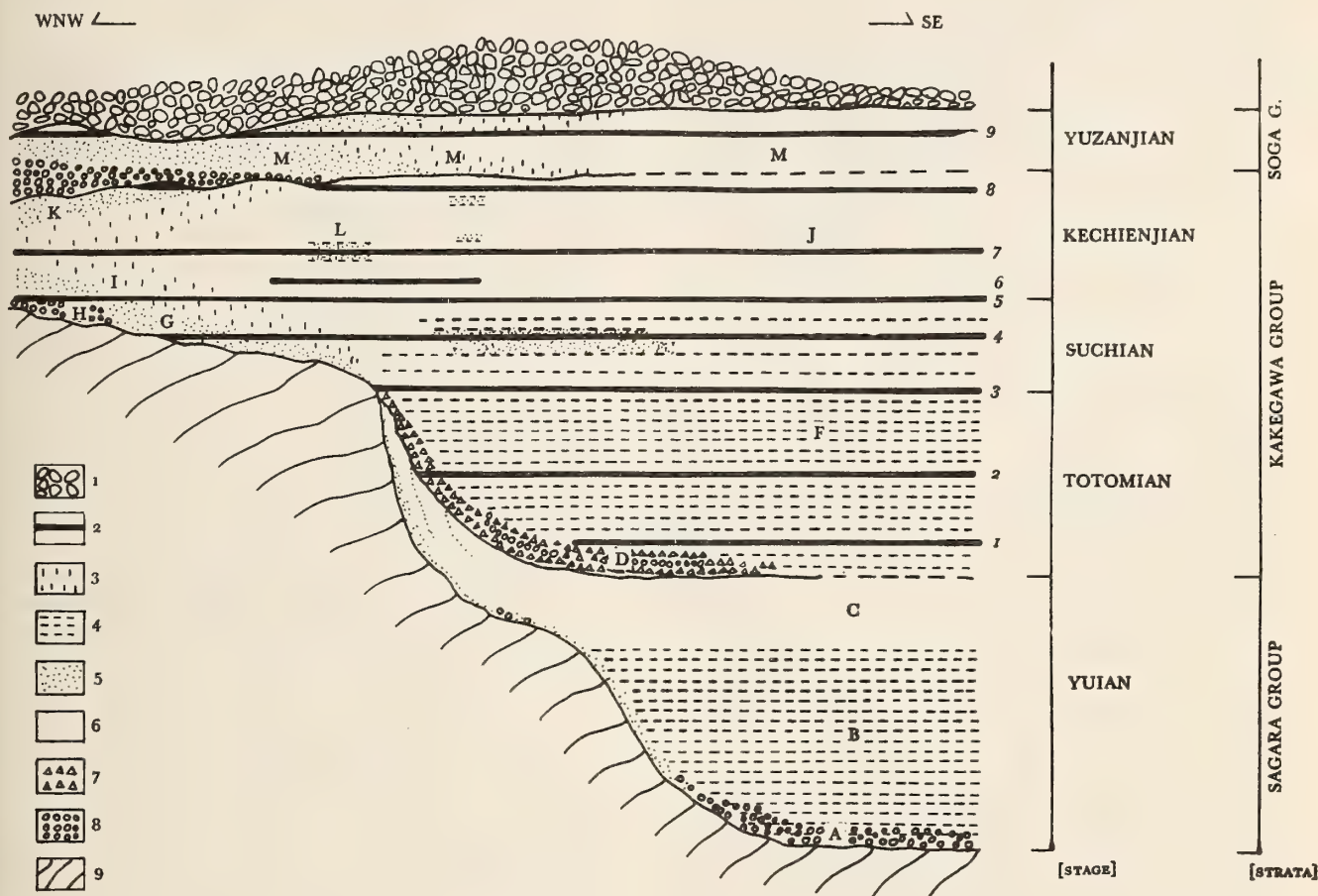


Figure 3

Idealized profile of the late Neogene series of the Kakegawa district
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 Group (gravels, sand and silt).

geological map and the stratigraphic sequence in the profile are shown in Figures 2 and 3. The late Neogene series, consisting of the Sagara, Kakegawa and Soga Groups, overlies the early Neogene series with marked unconformity and is covered by the Pleistocene Ogasayama Gravels. The Kakegawa Group lies on the Sagara Group with local unconformity in the north, and the Soga Group also lies on the Kakegawa Group with local disconformity in the north. Thus, each group reveals a sedimentary cycle with shallow deposits in its basal part and is superposed on the underlying group with an unconformable relation in the north, that is, paleogeographically landward, but in the south, that is, offshore at that time, they represent continuous sedimentation.

The Sagara Group, the main extension of which is in the eastern Omaesaki Peninsula, consists of a thick rhythmic alternation of sand and silt (Sagara Alternation) in the lower part, with frequent intercalations of granule beds near the base (Tokigaya Alternation), and a massive homogeneous silt (Oyori Silt) in the upper part. Only the upper silt member extends to the north and northwest, where the silt is found exposed as an inlier (Tamari Silt). The thickness of the group ranges from 1500 m in the south to 400 m or so in the north.

The Kakegawa Group shows a remarkable contrast in lithofacies between the eastern and western exposures. In the east, a thick rhythmic alternation of sand and silt (Horinouchi Alternation), and a stratified conglomerate bed (Hagima Conglomerate) are predominant in the lower part and a massive homogeneous silt bed (Hijikata Silt) in the upper part. Such a succession resembles that of the Sagara Group. The Hagima Conglomerate in the east is the basal conglomerate of the Kakegawa Group, but in the north it represents a basal unit of a transgressive overlapping of the Horinouchi Alternation onto the basement, where it corresponds in age to approximately the whole Horinouchi Alternation. The conglomerate overlies the Sagara Group with unconformity in the north, while in the south it merely represents a transitional bed between the Sagara and Kakegawa Groups, where the conglomerate grades into alternations of sand and granule beds, or thick sand layers. The Horinouchi Member is a rhythmic alternation of sand and silt, which attains a thickness of 3500 m in the depocentre near Kikugawa, but becomes thinner towards the northwest and the southeast. The facies of the Kakegawa Group in the west should probably be called a coastal oscillation facies, as compared with the above-mentioned flysch-type facies in the east. A complete sedimentary cycle is found in the vicinity of Kakegawa in a succession of sand (Dainichi Sand), silty sand (Tenno Silty Sand), silt (Hijikata Silt), silty sand (Tenno Silty Sand),

and sand (Aburayama Sand), in ascending order. It is found also in the western end on the left side of Tenryu River in a succession of conglomerate (Nobe Conglomerate), sand (Dainichi Sand), silty sand (Tenno Silty Sand), and sand (Aburayama Sand), where the Hijikata Silt thins out. The Kakegawa Group accumulated first by geosynclinal subsidence of the Kikugawa basin, where the thick flysch-type sequence exists, then, the sea gradually invaded the stable area to the west, where the coastal oscillation facies is seen.

The Soga Group, which overlies the Kakegawa Group with local disconformity in the northwest, consists of a sedimentary cycle with gravels, sand and silt in the northern area. In the southern area, however, it consists of massive homogeneous silt which is quite similar to, and continuous with, the Hijikata Silt of the Kakegawa Group. Therefore, the lower boundary in the south is defined for convenience between the uppermost pyroclastic layer of the Kakegawa Group (Kogoshō Tuff) and the lowest pyroclastic layer of the Soga Group (Soga Tuff).

Many white-coloured fine-grained acidic tuff layers in the Kakegawa and Soga Groups are keys to chronostratigraphic subdivision. Important pyroclastic layers are named in ascending order as follows: Arigaya, Shiraiwa, Iozumi, Nishihirao, Agehari, Hosoya, Nishi-Kakegawa, Sakuragi, Kogoshō, and Soga, respectively. As clearly demonstrated on the geological map and also in the profile, the time-stratigraphic markers intersect the rock facies divisions.

Concerning the geologic structure, the Sagara Group exhibits a folded structure with a NE-SW trend in the southeast, where several brachy-anticlines and brachy-synclines are found *pari passu*. The NE-SW trend of the structure abruptly turns in the north to the E-W trend with a southward dip. The Kakegawa Group displays a monoclinical structure with the NW-SE trend in the east dipping to the southwest at about 15 degrees, where the trend is oblique to that of the underlying Sagara Group, but in the southeastern area, the trend turns gradually to NE-SW, where the structure becomes concordant with that of the Sagara Group. The strong inclination of the Horinouchi Alternation in the southeastern area decreases upward. The Kakegawa Group in the west trends from ESE to WNW showing a homoclinal structure dipping to SSW at about 8 degrees. The structure of the Soga Group is concordant to the Kakegawa Group. Therefore, it is noteworthy that the local disconformity at the base of the Soga Group indicates a kind of epeirogenic fluctuation, presenting a marked contrast to the local unconformity at the base of the Kakegawa Group which evidently resulted

from the crustal movement followed by a shifting of the basin.

MOLLUSCAN FAUNAL SUCCESSION

The Kakegawa molluscan fauna, studied by YOKOYAMA (1923, 1926), MAKIYAMA (1925, 1927, 1931, 1941b, 1952) and TSUCHI (1961, 1969), is known as the best representative of the Pliocene of the Pacific coast of southwestern Japan. The Sagara molluscan fauna is characterized by *Amussiopecten iitomiensis* (Otuka), *Chlamys miurensis* (Yokoyama), etc. The Kakegawa fauna comprises *Amussiopecten praesignis* (Yokoyama), *Venericardia panda* (Yokoyama),

Suchium suchiense (Yokoyama), *Turritella perterebra* (Yokoyama), *Siphonalia declivis* (Yokoyama) and many other warm current and tropical forms, 50% of which are extinct species. The Soga fauna consists mostly of Recent species which are now living in the adjacent sea. From the viewpoint of chronostratigraphic subdivision, the stratigraphic sequence of the late Neogene series can be divided by molluscan faunal changes into the following five stages in ascending order.

- 5) Yuzanjian
- 4) Kechienjian
- 3) Suchian
- 2) Totomian
- 1) Yuian
- (Soga Group)
- (Kakegawa Group)
- (Sagara Group)

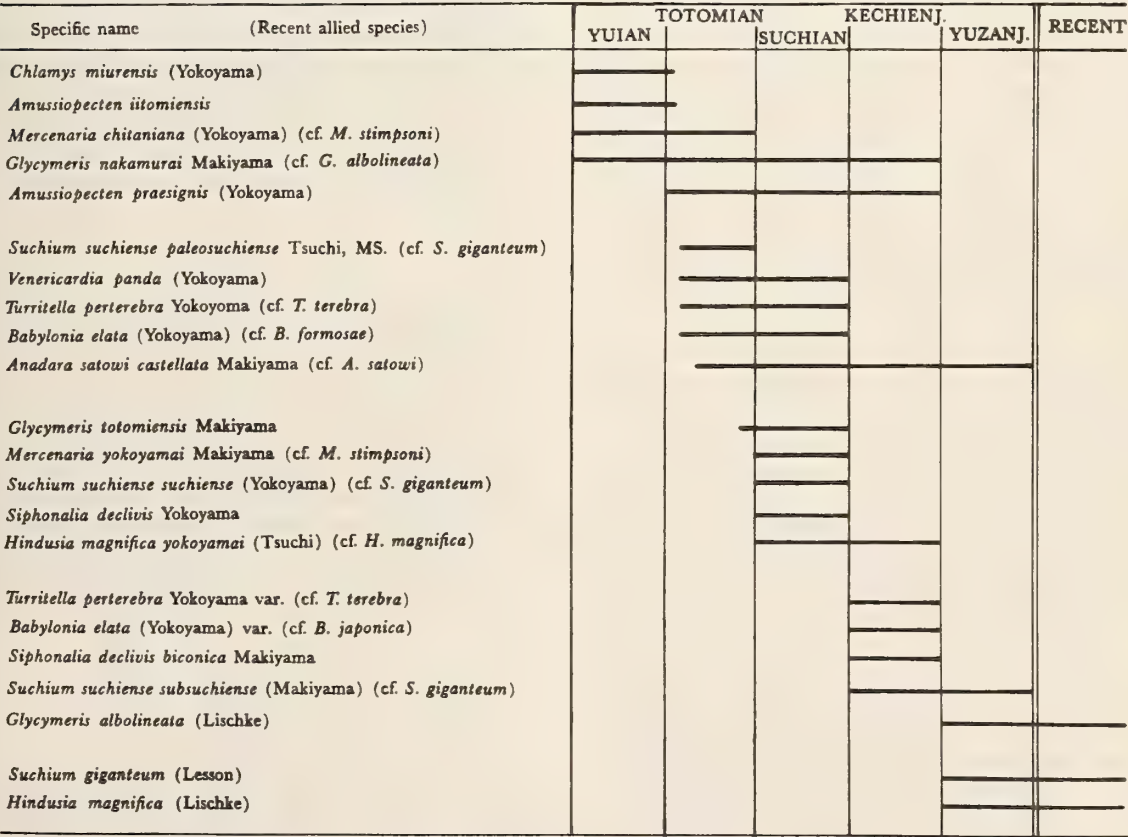


Figure 4
Stratigraphic range chart of important molluscan species and sub-species of the late Neogene series of the Kakegawa district.

The bases of the Suchian and the Kechienjian are, for convenience, defined by pyroclastic layers just below fossil localities and assigned, respectively, to the basal horizons of the Iozumi Tuff and the Hosoya Tuff. The definitions of the Yuian, Suchian, Kechienjian and Yuzanjan stages which were proposed originally by MAKIYAMA (1931, 1941a), and MAKIYAMA & SAKAMOTO (1957) have been amended by TSUCHI (1961). The Totomian Stage was proposed by TSUCHI (1961). Thus, the Horinouchi Alternation nearly belongs to both the Totomian and Suchian Stages, the Hijikata Silt to both the Kechienjian and Yuzanjan Stages and the Dainichi Sand facies corresponds to both the Suchian and early Kechienjian Stages, i. e., the middle and upper parts of the Kakegawa Group.

Vertical ranges of the important molluscan species are shown in Figure 4. The combination of genera or species of one stage is essentially similar to another. This means that similar conditions continued for a long time throughout this sequence of stages. A faunal change between two successive stages means the appearance or disappearance of a species or subspecies, especially by the replacement of a form by an allied one. The major faunal changes are, however, recognized between the stratigraphic cycles. That is to say, the rise and fall of the fauna seem to be inseparable from the sedimentary cycles. Here, the Sagara, Kakegawa and post-Kakegawa (living form) faunas which the authors propose are such major faunas. The vertical succession of the faunas in respective stages are as follows:

- 5) Yuzanjan Stage: The coexistence of the Kakegawa relics with living species which amount to 90% of the fauna.
- 4) Kechienjian Stage: The disappearance of some Kakegawa members and slight modification of some others.
- 3) Suchian Stage: The acme of the Kakegawa fauna.
- 2) Totomian Stage: The appearance of a few Kakegawa members coexisting with Sagara relics.
- 1) Yuian Stage: This is represented by the flourishing of the Sagara fauna.

The whole fauna of the Kakegawa district has a combination of genera and species that is similar to the present open coastal community on the Pacific coast of southwestern Japan. Accordingly, the open coast must have been similarly affected [controlled] by the warm Kuroshio current in the late Neogene period just as it is today. Therefore, the faunal changes in the succession depend on either minor changes of the environment, or probably, organic evolution. This is well demonstrated by a series of *Suchium suchiense*, a typical japonic endemic form, that range from the Totomian stage through the Suchian and Kechienjian

to the Yuzanjan Stage. This series includes *S. suchiense paleosuchiense* Tsuchi MS. of the Totomian, *S. suchiense s.s* (Yokoyama), of the Suchian, and *S. suchiense subsuchiense* (Makiyama) of the Kechienjian and Yuzanjan, which are trochid gastropods having spiral striae on the surface, and tubercles on the subsutural band. As the surface features in the bio-series gradually change from one subspecies to another, the series can be considered as a successional species (TSUCHI, 1969). *Suchium giganteum* (Lesson), a living species with a smooth surface with a few feeble striae on the peripheral margin, appeared in the Yuzanjan; this species flourishes in the later part of the stage.

One of the characteristics of the Sagara and Kakegawa faunas is the inclusion of rich tropical elements, which are not found in adjacent seas. For example, recent species allied to *Venericardia panda* (Yokoyama), *Turritella perterebra* (Yokoyama) and *Babylonia elata* (Yokoyama) are living on the coast south of Formosa. Allied Neogene forms of *Amusiopecten* occur in Formosa, Timor and Java. *Nassarius*, *Hindsia* and *Babylonia* bear canaliculate shoulders and other similar features of allied forms living in tropical seas. These tropical elements abruptly decline in the Kechienjian and all of them disappear by the end of the Kechienjian, when some thermal fluctuations probably occurred.

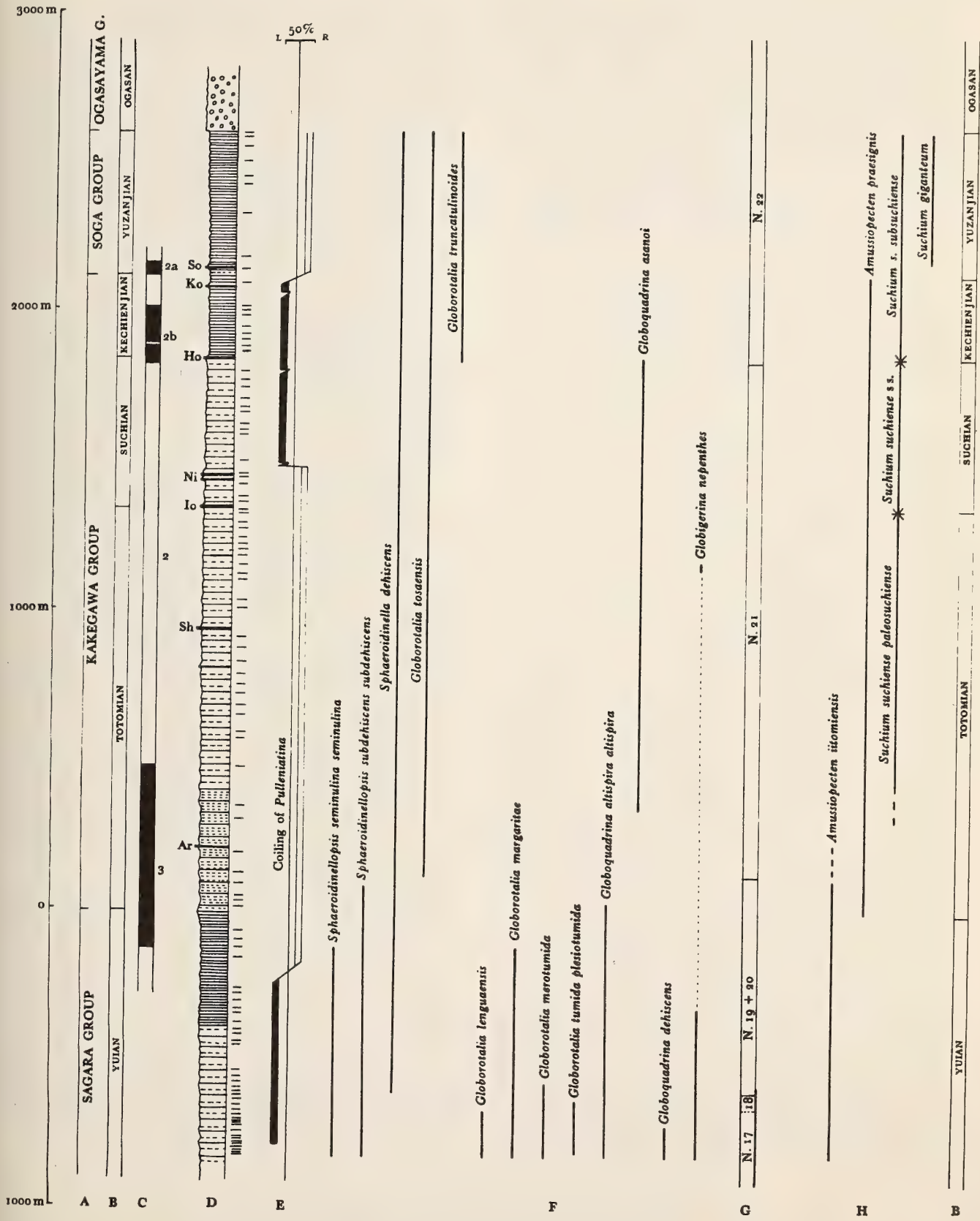
PLANKTONIC FORAMINIFERAL BIOSTRATIGRAPHY AND RELATION TO MOLLUSCAN STAGES

Planktonic foraminiferal biostratigraphy of the late Neogene series has been studied by SAITO (1960) and several others. ODA (1971) confirmed that the biostratigraphic classification of the Sagara Group by planktonic foraminifera corresponds well to zones established originally in the tropical region by BLOW (1969). According to UJIE & HARIU

(on facing page →)

Figure 5

Columnar section of the late Neogene series of the Kakegawa district, with reference to vertical ranges of selected molluscan and planktonic foraminiferal species, and magnetostratigraphy. A: Strata. B: Stage. C: Magnetozone. D: Columnar section (Tuff: Ar - Arigaya; SH - Shiraiwa; Io - Iozumi; Ni - Nishihirao; Ho - Hosoya; Ko - Kogoshō; So - Soga). E: Coiling of *Puleniatina* complex. F: Vertical range of selected planktonic foraminifera. G: Planktonic foraminiferal zone. H: Vertical range of selected molluscan species.



(1975), the Sagara Group belongs to Zone N.14-N.19 ranging in age from the latest middle Miocene to early Pliocene. In the Kakegawa Group, Zones N.19-N.22 have been recognized by MOROZUMI (1972) and KATO (1973). From the viewpoint of planktonic foraminifera, therefore, the Miocene/Pliocene and Pliocene/Pleistocene boundaries might be defined in the upper part of the Sagara Group and in the upper part of the Kakegawa Group, respectively.

The planktonic foraminiferal biostratigraphy of the district was also investigated recently by the authors, especially in sections of southern offshore facies (IBARAKI & TSUCHI, 1974, 1976; TSUCHI & IBARAKI, 1977a). The relation of the planktonic foraminiferal sequence to the molluscan stages can be clearly ascertained by means of intercalated pyroclastic layers which occur throughout the northern nearshore and southern offshore facies. Magnetostratigraphic surveys were also made by YOSHIDA & NIITSUMA (1976) on the same routes and sections. Results of those investigations are shown in Figure 5, in which vertical ranges of selected planktonic foraminiferal and molluscan species important for zoning are arranged.

The first occurrence of *Sphaeroidinella dehiscens* (Parker & Jones) which defines the base of Zone N.19 is recognized in the middle of the Sagara Group, or in the middle Yuian Stage. *Globorotalia tosaensis* Takayanagi & Saito makes its initial evolutionary appearance at a horizon 120 m above the base of the Kakegawa Group and a little below the Arigaya Tuff in the basal part of the Kakegawa Group, or in the earliest Totomian. And *Globorotalia truncatulinoides* (D'Orbigny) initially appears at a horizon just below the Hosoya Tuff, i.e., nearly at the base of the Kechienjian. Thus, the bases of Zones N.21 and N.22 are defined, respectively by initial appearances of these species. Based on the successive appearance of *Sphaeroidinella dehiscens*, *Globorotalia tosaensis* and *G. truncatulinoides*, horizons of the later half of the Yuian Stage and the earliest part of the Totomian, those of most of the Totomian and Suchian, and both the Kechienjian and the Yuzanjan are assigned, respectively, to Zones N.19+20, N.21 and N.22. *Globorotalia quadrina asanoi* Maiya, Saito & Sato ranges from a horizon a little above the initial appearance of *Globorotalia tosaensis* to a horizon a little above the first appearance of *G. truncatulinoides*, corresponding to horizons from the earliest part of the Totomian to the earliest part of the Kechienjian. The vertical range of the species has been recognized from the middle of the Gauss Normal Epoch to the base of the Olduvai Event in the North Pacific deep sea cores, and the specimens have also been found abundantly in the upper part of the Funakawa Formation of the Oga Peninsula on the Japan Sea coast, being restricted to the *Globigerina pachyderma* (dextral)/*Globorotalia orientalis* Zone (MAIYA, SAITO & SATO, 1976). Thus, the species is

important in the correlation of the Neogene of the Pacific coast with that of the Japan Sea coast and North Pacific deep sea sediments.

Abrupt changes in coiling direction of the *Pulleniatina* complex from sinistral to dextral recognized in the late Yuian, from dextral to sinistral in the early Suchian, and from sinistral to dextral at the beginning of the Yuzanjan are noticeable. Partial changes of the coiling ratio are found in a horizon following the abrupt change from dextral to sinistral in the early Suchian, and also in two horizons of the late Suchian and late Kechienjian.

The magnetozones recognized in the Kakegawa Group can be correlated with magnetic polarity intervals established in deep sea sediments (OPDYKE *et al.*, 1974), by considering the interrelation between the biostratigraphy and magnetostratigraphy of deep sea cores (HAYS *et al.*, 1969). A normally magnetized interval found in horizons below the middle Totomian can be correlated with the Magnetic Interval 3 or "Gauss Normal Epoch," a predominantly reversed magnetized interval in horizons above the middle Totomian with the Magnetic Interval 2 or "Matuyama Reversed Epoch," and a predominantly normally magnetized interval of the early Kechienjian with the Subinterval 2-b or "Olduvai Normal Event." The initial appearance of *Globorotalia tosaensis* in the Gauss Normal Epoch, and of *G. truncatulinoides* in the basal part of the Olduvai Normal Event, and the aspect of coiling changes of *Pulleniatina* correspond well to the record in equatorial Pacific deep sea cores (HAYS *et al.*, 1969). The Neogene-Quaternary boundary might be placed, at present, at or near the base of the Kechienjian Stage (IKEBE & TSUCHI, 1977; TSUCHI & IBARAKI, 1977b).

From the ratio of tropical and subarctic species to the total population, the temperature of the seawater during the Kakegawa Age might not be very different from that of the present adjacent sea, but a cooling of seawater temperature since the latest Kechienjian is suggested. This fact seems to match well with the disappearance of tropical mollusks by the end of the Kechienjian.

Radiometric age determinations by the fission track method have been attempted on some pyroclastic layers of the Kakegawa Group. The Arigaya, Iozumi and Hosoya Tuff beds have been dated, respectively, at 5.8×10^6 y. B. P., 2.8×10^6 y. B. P. and 2.2×10^6 y. B. P. (NISHIMURA, 1975). According to Dr. S. Nishimura of Kyoto University (oral communication), however, the above-mentioned datings may change to younger values based on recent re-examination. From the magnetostratigraphy and radiometric ages, an estimation of the evolutionary rate of speciation in *Suchium* and some other Mollusca and planktonic foraminifera can be made.

As the chronostratigraphic subdivision of the late Neogene series of the Kakegawa district can be discriminated through late Neogene sections on the Pacific coast of southwestern Japan, the above-mentioned interrelation between molluscan stages and planktonic foraminiferal zones seems to be applicable throughout the region. A correlation chart of late Neogene sediments on the Pacific coast of southwestern Japan is shown in Figure 6. The planktonic foraminiferal sequence and its relation to molluscan stages have been ascertained by the authors in a section in the southern Okinawa Island (IBARAKI & TSUCHI, 1975).

SUMMARY

Study of the late Neogene molluscan faunal succession in nearshore sections and the planktonic foraminiferal sequence in offshore sections of the Kakegawa district has demonstrated the interrelationship between molluscan

stages and worldwide planktonic foraminiferal zones. This interrelationship seems to be applicable in late Neogene sections throughout the Pacific coast of southwestern Japan. A series of five molluscan stages is shown to correspond to BLOW's (1969) Neogene planktonic foraminiferal zones N.14 through N.22. The Neogene/Quaternary boundary can be placed at or near the base of the Kechienjia Stage. A cooling of seawater temperature since the latest Kechienjia found in planktonic foraminiferal populations is also recognized in the molluscan faunal succession.

ACKNOWLEDGMENT

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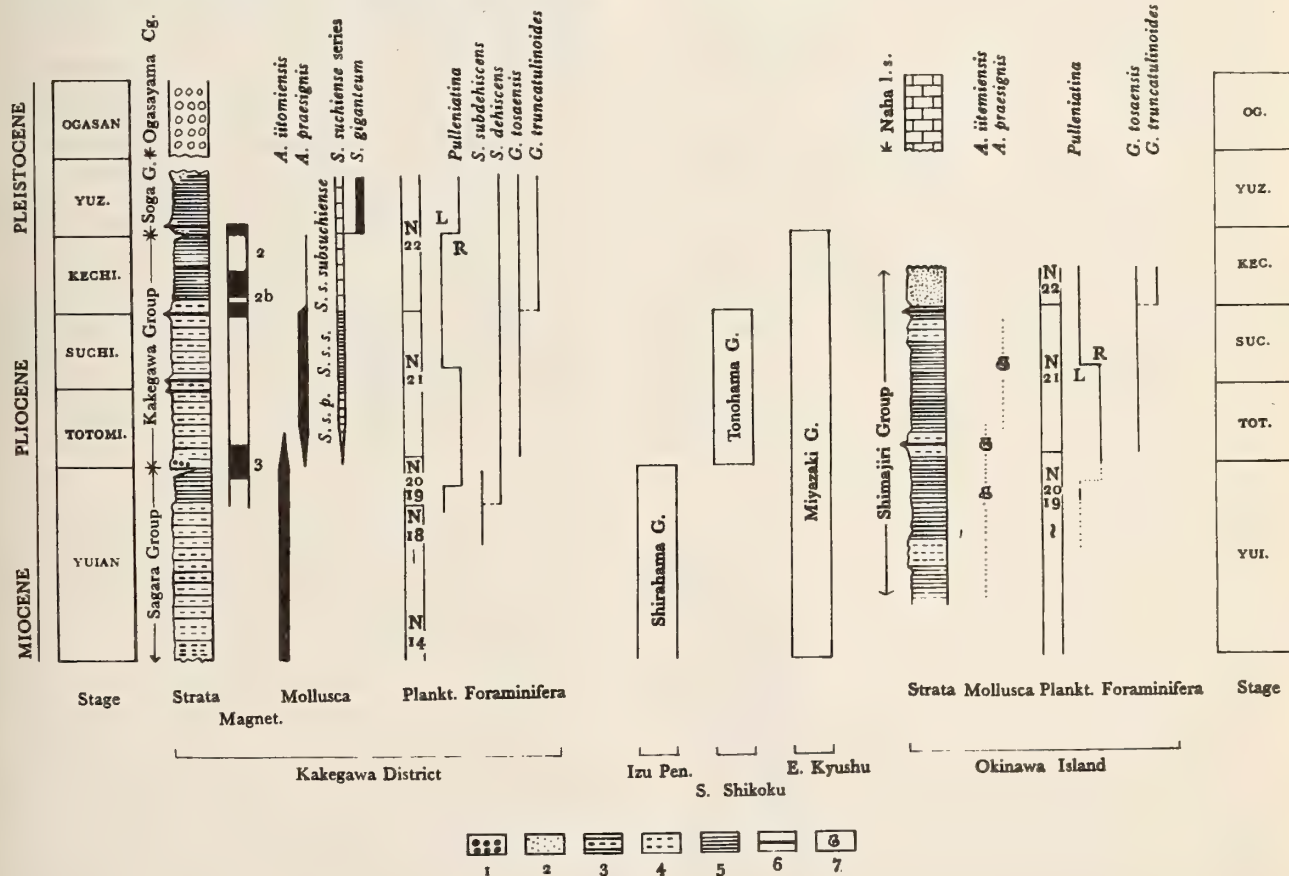


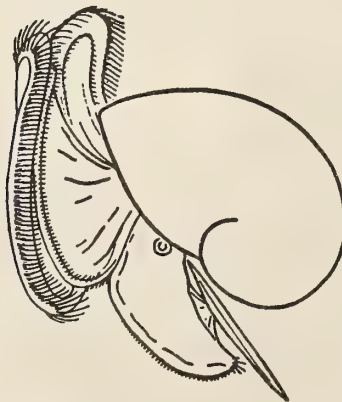
Figure 6

Correlation chart of late Neogene sediments on the Pacific coast of southwestern Japan, especially between the Kakegawa district and the Okinawa Island.

1: Conglomerate. 2: Sand. 3: Alternation of sand and silt. 4: Silty sand. 5: Silt. 6: Pyroclastic layer. 7: Occurrence of Mollusca.

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Premises of Neogene Correlation in the Northern Part of the Circum-Pacific

BY

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CONSIDERABLE ADVANCES have been achieved in subdivision of the marine Neogene of the northern part of the Circum-Pacific area. This problem was rather thoroughly elucidated at the First International Congress on Pacific Neogene Stratigraphy held in Tokyo in 1976 (SAITO & UJIE, 1977). Nevertheless, there are still many questions that remain obscure. That is why I should like to concentrate upon some general points including some of the difficulties we may face in correlating the marine Cenozoic of northern regions.

It is well known that remains of the fossil groups usually used for subdividing the stratigraphic sections in the Arctic and Boreal regions are not considered reliable for long distance correlations due to their strong dependence upon facies conditions. These kinds of fossils are: mollusks, benthonic foraminifers, echinoids, and plant remains. The use of these groups allows us, in fact, to compile only regional stratigraphic schemes. Unfortunately the more widespread fossil groups such as planktonic foraminifers and nannoplankton that are so effectively used in lower latitudes are rarely observed in the Arctic and Boreal regions.

Secondly, I want to emphasize the fact that until recently lithostratigraphic subdivisions such as formations and suites have been mapped in many countries. Analysis shows that their boundaries are frequently diachronous and this, naturally, makes correlation difficult. Many papers devoted to this problem have been written in the Soviet Union, North America, and Japan.

Hence, these essential conclusions follow. First of all, we have to compile regional stratigraphic schemes using the "working" paleontological groups that exist, in fact (benthonic organisms, in particular), in every region. In order to single out chronostratigraphic subdivisions, such as horizons or regiostages, but not lithostratigraphic ones, we should use such a change of assemblages that would be specified, first of all, by the evolutionary stages of these groups and stages of development of the basin. The regional sequences are compiled in various climatic zones and in areas with different geological histories.

The second task is correlation of these sequences with one another, and then correlation of these with the time scales of warm-water areas. Such a correlation can provide a reliable age determination of horizons, and, as a result, can help in deciphering geological events of the past. At present we use various groups, such as mollusks, foraminifers, and diatoms as well as climatic datum remarks, for interregional correlations. True, their correlative role is frequently effective at only certain levels, but abundant materials from various regions give us hope that these correlations will be gradually perfected.

The study of fossil faunas from the North Pacific shows that we can now outline a number of levels that can be traced from Alaska and Chukotka southeastward to California and southwestward to Japan (GLADENKOV, 1977). For example, the upper Paleogene horizon including the bivalve mollusks *Papyridea harrimani* Dall, *Yoldia watasei* Kanehara, etc., is well observed in Kamchatka, Sakhalin, Japan, and possibly in North America. The lower Pliocene horizon with the bivalves *Fortipecten takahashii* (Yokoyama) and *F. hallae* (Dall) and often with the diatom *Denticula kamtschatica* Zabelina, etc., and the Pleistocene horizon (with the bivalve *Portlandia arctica* Gray and Recent assemblages) are well pronounced in all of the regions mentioned above.

Some of the other levels distinguished by means of various fossil groups were observed in only two or three regions. They are:

- 1) The lower Miocene level with the bivalves *Yoldia tokunagai* Yokoyama and *Malletia intermis* Yokoyama which can be recognized in northern Japan, Sakhalin, and Kamchatka.

- 2) The middle Miocene level containing the diatoms *Stephanopyxis schenckii* Kanaya and *Denticula lauta* Bailey, the foraminifer *Ammonia tochiensis* (Uchio) is found in Japan, Sakhalin, and Kamchatka. In Sakhalin the planktonic foraminifer *Globorotalia linguaensis* Bolli appears to be confined to this level.

- 3) The middle Miocene level with the foraminifers *Brizalina pseudospissa* Kleinpell and *Cibicides altamira-*

ensis Kleinpell, and the bivalve *Securella panzana* (Anderson & Martin) has been recognized in California and in Kamchatka.

4) The upper Miocene level with the bivalve *Mytiloconcha coalingensis* (Arnold), etc., can be identified in California and in Kamchatka.

5) An upper Pliocene horizon with the bivalve *Astarte diversa* Dall and the diatom *Melosira albicans* Sheshukova can be recognized in Alaska and in Kamchatka.

In all of these regions a horizon associated with the climatic optimum of the middle Miocene can also be recognized. This level is identified by a high percentage of *Fagus* in palynological spectra as well as by other changes in the fossil flora and fauna.

The correlation of regional horizons with the world-wide sequence is rather tentative as yet. Planktonic calcareous microfaunas present in some layers are certain to aid in correlation, but the most precise data are likely to be obtained through study of groups with siliceous skeletons. So, these groups are currently the focus of attention. In some cases paleomagnetic data and radiological dating are used for correlation. But, at the present time, these data are not numerous.

As for the correlation with the world-wide Neogene scale, of paramount importance are the fossil faunas from Japan and California. These have an intermediate position between the sequences of the Boreal region to the north and warm water regions to the south.

If there are no data for direct correlation of the regional schemes for various regions, each of the sequences can be correlated separately with the world-wide Neogene scale. With these results, the regional scales can then be corre-

lated with each other. Such correlations, though logical, are indirect and have to be carefully checked.

In 1976 at the First International Congress on the Pacific Neogene Stratigraphy, the Working Group of Chronostratigraphy of the North Pacific was organized (ARMENTROUT, 1977). This group was an outgrowth of the technical sessions on Mollusca. The papers from this session are to be found elsewhere in this issue. The program of this group, formulated by Dr. R. C. Allison and myself, is aimed at compilation of detailed regional sequences of on-shore marine basins followed by the description of regional stages and analysis of their paleontological characteristics. Also of importance is the correlation of regional sequences of various regions and comparison of them with the Neogene scale of warm water areas. It is anticipated that scientists from the Soviet Union, the United States, Canada, Mexico, and Japan will participate in this joint effort. It is hoped that this cooperation will facilitate the compilation of a universal Cenozoic scale, for the entire Pacific sector. Geological theory and practice have been in need of such a scale.

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History of the Pliocene Molluscan Fauna of Northern Japan

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(1 Text figure)

INTRODUCTION

AS A STEP IN UNDERSTANDING the origin of the modern North Pacific molluscan fauna, a study of the Pliocene molluscan fauna of northern Japan was undertaken. The principal aim of the study was to interpret the probable areas of origin and the dispersal history of bivalve and gastropod genera and subgenera which make up that fauna. Brief comments concerning development of the Japanese Cenozoic molluscan fauna and a comparison of Tethyan immigrant history in Japan and New Zealand are included.

The findings in this study are based on 126 taxa including 107 genera and 19 subgenera. Taxonomic designations and age assignments by previous workers were generally followed because a comprehensive re-evaluation of the literature was not possible within the scope of the study. Because there are gaps in the knowledge of some genera, the findings presented herein range from plausible to speculative. The place of earliest occurrence of fossil taxa and their chronologic and geographic distributions served as the principal bases for interpreting the place of origin and migratory history of mollusks.

Over 200 reports concerning the Mesozoic and Cenozoic molluscan records of the Pacific basin, and to a lesser extent those of the western Tethys and New World, were examined. Only those papers essential to the preparation of this report have been cited. The major works on Jurassic and Cretaceous bivalves by HAYAMI (1961, 1965 and 1966) and the Paleogene molluscan record by OYAMA, MIZUNO & SAKAMOTO (1960) were especially useful for the pre-Neogene molluscan record in Japan. Sources which were important in gleaning the Neogene molluscan record of Japan include check lists of Japanese Cenozoic marine mollusca by HATAI & NISIYAMA (1952) and MASUDA & NODA (1976); additional pertinent references are to be found in the bibliographies of these works. The Treatise of Inverte-

brate Paleontology (Part N. vols. 1, 2 and 3; MOORE, R.C., 1969) served as a basic source for systematic biogeographic and chronologic information for bivalves; WENZ (1938-44) and KEEN (1963) served in a similar way for gastropods.

The results of this study, in summary form, show only general trends concerning the provenance of Pliocene bivalve and gastropod genera of northern Japan. It is hoped that the study will be stimulating and form a useful basis for more refined studies of this fascinating subject.

THE PLIOCENE FAUNA

The Pliocene fauna of this study is an artificial aggregate of molluscan assemblages from major Pliocene deposits of northernmost Honshu and Hokkaido. The Honshu assemblages were described from stratigraphic units exposed in Aomori Prefecture at the extreme north end of Honshu Island. These deposits and the citations followed in this study include: (1) Sannohe Group (CHINZEI 1959, 1961) and (2) Narusewa, Higashimeya, Totezawa, and Dai-shaka formations of the Tsugaru sequence (Iwai, 1965). The Hokkaido assemblages were described from the Setana Formation (Uozumi, 1962; Kanno, 1962) and the Takikawa Formation (Uozumi, 1962). The fauna of the Hamada Formation (Hatai, Masuda & Suzuki, 1961) of Aomori Prefecture was not considered in this paper but the majority of its bivalve and gastropod genera is represented in the fauna herein delineated. The Pliocene fauna reflects a variety of marine environments ranging from shallow to deep water facies and represents molluscan life in 4 or 5 marine basins. On the whole, the generic and subgeneric composition of the fauna is similar to that of the northern temperate/boreal regions of the North Pacific, with some elements more characteristic of lower latitudes present. No attempt was made to subdivide the fauna in a time-stratigraphic sense.

MESOZOIC ROOTS

A number of genera and subgenera found in the Pliocene fauna of northern Japan were residents of Japanese waters as early as Jurassic and Cretaceous times (22; 17%). The following genera are present in the Jurassic record: *Nuculana*, *Solemya*, *Modiolus*, *Lima*, *Limatula*, *Astarte*, *Ostrea*, *Cuspidaria*, *Pholadomya*, *Thracia*, and *Mytilus*. Genera which evidently made first appearances in Japanese seas during Cretaceous times include: *Acila* (*Truncacila*), *Yoldia*, *Glycymeris*, *Chlamys*, *Barbatia*, *Nemocardium*, *Panope*, *Tellina*, *Spondylus*, *Turritella*, and *Cerithium*. Other genera have been reported from the Cretaceous of Japan but their generic assignments are considered doubtful. These "Cretaceous" genera and their probable earliest valid occurrences in Japan are: (1) Eocene - *Siliqua*, *Anomia*, and *Callista*; (2) Oligocene - *Portlandia*, *Arca*, *Monia*, *Lucinoma*, *Laevicardium*, *Spisula*, and *Epitonium*; (3) Miocene - *Chama* and *Natica*.

Of the Jurassic and Cretaceous taxa herein considered to be valid residents of Japan during the Mesozoic, a few have histories extending much farther back in time in other parts of the world including *Solemya* (Devonian), *Modiolus* (Devonian), and *Pholadomya* (Triassic). The first Japanese occurrences of the balance of the Mesozoic genera and subgenera, however, very closely approximate their earliest known occurrences elsewhere in the world. Virtually all of the Mesozoic genera and subgenera have rather cosmopolitan fossil records so that, at present, there is no strong basis for identifying a relatively specific geographic place of origin for any of them. Many of these genera have substantial distributions in the Tethyan region. Judging from their extensive Cenozoic fossil records in Japan, these taxa have evidently persisted in Japanese waters from Mesozoic time up to the present. It is possible that other populations, representing the same genera that lived in Cretaceous and Jurassic seas of Japan, may have been re-introduced to Japan through migration during the Cenozoic. The apparent lack of a fossil record between Cretaceous and early Miocene time suggests that *Limatula* and *Spondylus* may represent two such populations.

CENOZOIC HISTORY

The overwhelming majority of genera and subgenera (109; 84%) making up the Pliocene fauna of northern Japan were introduced into Japanese seas during the Cenozoic Era. Source areas include the North Pacific (42%), Tethyan region (40%) and possibly the Atlantic basin (1%).

NORTH PACIFIC INFLUENCE

North Pacific genera and subgenera include: (1) those that evolved in Japanese waters or close to them, (2) those that evolved in the eastern North Pacific and migrated to Japan, and (3) those that evolved in the North Pacific realm but whose specific place of origin is not clear.

Genera and subgenera believed to have originated in Japanese waters, or close by, and their probable times of origin are: Eocene - *Neptunea*; Oligocene - *Mya*; Miocene - *Mizuhopecten*, *Fortipecten*, *Swiftopecten*, *Kotorapecten*, *Placopecten*, *Coraeophos*, *Protothaca* (*Callichaca*); Pliocene - *Yabepecten*, *Turritella* (*Neohaustator*), *T.* (*Hataiella*) and *Dosinia* (*Kaneharaia*).

The fossil record of at least 4 genera seems to favor an origin somewhere in the northeastern Pacific region followed by westward migration to Japan; these genera and subgenera, and their earliest definite occurrences in Japan, are: Oligocene - *Fulgoraria*; Miocene - *Trichotropis*, *Fusitriton*; Pliocene - "Macron." All of these genera occur earlier in the eastern Pacific by, at least, one full epoch.

The area of origin of the balance of North Pacific genera and subgenera cannot be determined at this time. These taxa and their earliest occurrences in Japan are: Eocene - *Cyclina*, *Macoma*; Oligocene - *Acila* (*Acila*), *Thyasira* (*Conchocele*), *Clinocardium*, *Serripes*, *Spisula* (*Macromeris*), *Tellina* (*Peronidea*), *Epitonium* (*Boreoscala*), *Crepidula*, *Beringius*, *Buccinum*; Miocene - *Saxidomus*, *Tresus*, *Musculus*, *Panomya*, "Pandora", *Pholadidea*, *Puncturella*, *Menestho*, *Leucosyrinx*, *Lora*, *Natica* (*Cryptonatica*), *Trophonopsis*, *Nucella*, *Limopsis* (*Empleconia*); Pliocene - *Spisula* (*Pseudocardium*), *Fabulina*, *Ophioidermella*, *Liloea*, *Crepidatella*, *Mohnia*, *Colus*, *Suavodrilina*, *Antiplanes* (*Rectiplanes*) and *Propebela*.

TETHYAN INFLUENCE

The eastern Tethyan region furnished the following genera and subgenera at various times during the Cenozoic Era: Eocene - *Crenella*, *Mactra*, *Anomia*, *Siliqua*, *Callista*, *Lima* (*Acesta*), *Polinices*; Oligocene - *Spisula*, *Monia*, *Arca*, *Anadara*, *Septifer*, *Lucinoma*, *Venericardia* (*Cyclocardia*), *Laevicardium*, *L.* (*Fulvia*), *Dosinia*, *Meretrix*, *Clementia*, *Solen*, *Portlandia*, *Calliostoma*, *Nassarius*, *Epitonium*, *Hiatella*; Miocene - *Spondylus*, *Limatula*, *Pillucina*, *Chama*, *Venerupis*, *Pseudogrammatodon*, *Lithophaga*, *Mitrella*, *Olivella*, *Inquisitor*, *Bittium*, *Batillaria*, *Sinum*, *Cancellaria*, *Cocculina*, *Turcica*; Pliocene - *Nucinella* (*Huxleyia*), *Leptaxinus*, *Mysella*, *Gari*, *Dosina*

(*Phacosoma*), *Umbonium*, *Leptothyra*, *Serpulorbis*, *Alvania*, and *Fusinus*. The appearance of *Crenella* in the Eocene followed by a gap in the record until middle Miocene suggests that *Crenella* may have migrated to Japan on more than one occasion as has been suggested earlier in this paper for *Limatula* and *Spondylus*.

ATLANTIC INFLUENCE

The genus *Mercenaria* is represented in Japan by at least 4 species with an early Miocene to Recent time span. One species has also been reported in the northeastern Pacific but its occurrence there is regarded as of possible accidental origin (GRANT & GALE, 1931). In the northwestern Atlantic province, *Mercenaria* has a well-established history from Oligocene to Recent within a geographic span ranging from Nova Scotia to the Gulf of Mexico (PALMER, 1927). The earlier occurrence and development in the New World suggests that *Mercenaria* may have originated in the Gulf Coast area (Oligocene occurrences) and migrated to Japan via the Bering Sea in latest Oligocene/early Miocene time. If *Mercenaria* used the Bering Sea, then it would appear this dispersal route was open in late Oligocene-early Miocene time, which is earlier than the earliest Cenozoic (late Miocene) opening proposed by DURHAM & MACNEIL (1967). Other possible explanations for the apparent presence of *Mercenaria* in the western Pacific and Atlantic are: (1) polyphyletic origin, (2) migration into the western Pacific via Central America and the eastern Pacific, and (3) misidentification of fossils (not likely).

DISCUSSION AND SPECULATION

The above findings indicate that the generic and subgeneric composition of the fauna of northern Japan developed over a Jurassic-Pliocene time span from three main sources: (1) cosmopolitan Mesozoic holdovers of uncertain geographic provenance (17%), (2) North Pacific Cenozoic elements (42%), and (3) Tethyan immigrants of Cenozoic age (40%). A possible single Atlantic immigrant forms an additional Cenozoic source (1%). The Tethyan, North Pacific and Mesozoic elements are commonly associated at individual Pliocene fossil localities; no localities have been recognized in this study which are composed of genera and subgenera from a single source.

In terms of percentage of the total northern Pliocene fauna, the Tethyan (T) generic and subgeneric contribution appears to predominate over the North Pacific (NP) element during the Eocene (T-5%; NP-3%) and Oligo-

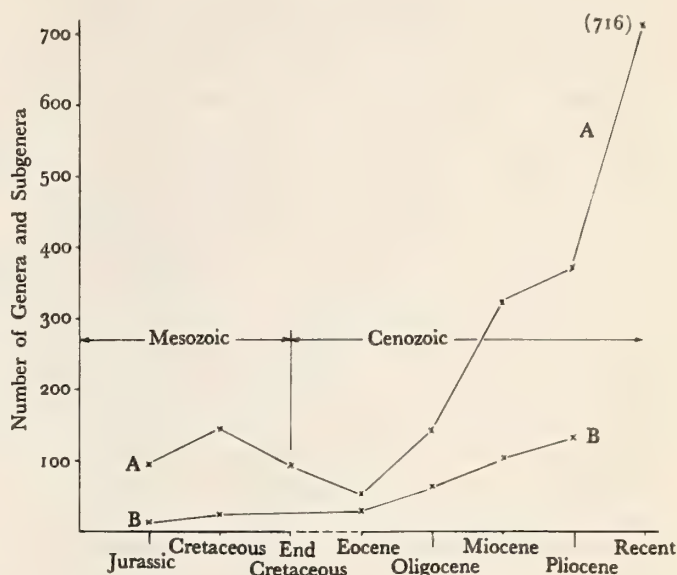


Figure 1

Comparison between (A) Diversity of total Japanese marine bivalve/gastropod fauna and (B) cumulative appearance of the northern Pliocene marine bivalve/gastropod fauna (The Paleocene is not generally recognized in Japan)

cene (T-15%; NP-10%); the North Pacific additions predominate in the Miocene (T-11%; NP-18%) and in the Pliocene (T-8%; NP-14%). The predominance of North Pacific elements in the Miocene and Pliocene may or may not be significant considering the size of the Pliocene fauna, but the figures are somewhat consistent with the consequences of the well-established southward shift of isotherms in the northeastern Pacific during the Cenozoic (DURHAM, 1950).

The appearance of genera and subgenera of the Pliocene fauna of northern Japan, as well as the generic diversity of the Japanese molluscan fauna (bivalves and gastropods combined), during the Mesozoic and Cenozoic Eras, is shown in Figure 1. The appearance of Pliocene genera mirrors the generic diversity of the total Japanese fauna, especially in terms of the fairly rapid and consistent increase during the Cenozoic. The total Japanese faunal diversity curve, however, reveals two features which are not reflected in the Pliocene curve.

The first of these is the sharp decline in the number of genera during the latest Mesozoic/earliest Cenozoic interval. This depletion of genera is probably a reflection of mass extinctions which took place on a world-wide scale at

the close of the Cretaceous. The second feature is the abrupt increase in numbers of genera/subgenera during the Oligocene/Miocene interval. This rapid increase may be the result of a combination of events related to the opening of the Sea of Japan and establishment of Japan as an island complex.

Japan, as now viewed within the context of plate tectonic theory, is thought to have been originally a coastal strip attached to the Asian continent just north of Korea (UYEDA & MIYASHIRO, 1974). Later, under the influence of tensional forces and sea-floor spreading, Japan was detached from the continent and carried eastward (300-800 km) with the Sea of Japan forming behind it. The rifting history is not well understood. UYEDA & MIYASHIRO (1974) consider rifting to have begun in Late Cretaceous/early Tertiary time; Dickinson (personal commun., 1977) believes that the Sea of Japan began to open sometime in post-Cretaceous time. HILDE & WAGEMAN (1973) have interpreted two spreading centers in the Sea of Japan of Late Cretaceous/early Tertiary and Miocene age; high heat flow in the Sea of Japan suggests that sea floor spreading may still be underway.

The early Tertiary fossil record in Japan suggests that from Eocene through Oligocene time, the Japanese region was progressively cooling from tropical to temperate conditions, a trend possibly related to the southern shift of isotherms interpreted by DURHAM (1950) for the north-eastern Pacific. Later, perhaps during latest Oligocene time, Japan was detached from the Asian coast and carried southeasterly directly into the path of the northeasterly flowing paleo-Kuroshio current which, presumably drew from warm equatorial waters of the southwest Pacific. Such a circumstance might then result in a change to subtropical and tropical conditions which indeed appear to characterize the middle Miocene of Japan (MINATO, GORAI & HUNASHI, 1965). Thus a part of the abrupt rise in molluscan genera during Oligocene/Miocene time may be attributable to rapid colonization by Tethyan immigrants following "intersection" of Japan and the warm, paleo-Kuroshio current, which would doubtless be carrying a stream of molluscan larva from the Tethyan region.

A second factor which may help explain the abrupt increase of genera during the Oligocene/Miocene interval, is the vast change in environmental conditions caused by changing from an unprotected, open coastal setting (before rifting) to that of a protected inland sea, flanked by a 2000 km-long archipelago (Japan) fronting on the open Pacific (after rifting). A vast new complex of shallow marine environments was almost surely created which in turn would act to heighten the potential for developing new genera through evolutionary processes as well as to provide a new

array of shallow water habitats not formerly available to existing genera and subgenera. The opening of new environments would be expected to increase the diversity of forms living in the region.

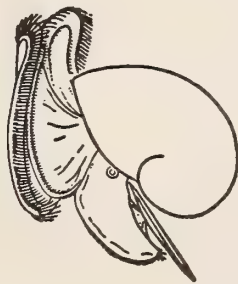
The roles of paleogeography, crustal movements, and current systems may help explain the Cenozoic molluscan history of New Zealand which is located in approximately the same latitudinal span in the southern hemisphere as Japan is in the northern hemisphere. FLEMING (1967) has shown that New Zealand, like Japan, received a strong influx of Tethyan bivalves and gastropods (about 169 genera) during the Cenozoic Era. Of special interest is the relatively high rate of extinction of Tethyan genera in New Zealand. According to FLEMING (*op. cit.*) about 65% (109) of all Tethyan immigrants reaching New Zealand during the Cenozoic became extinct before the end of that era, many dying out soon after their arrival in New Zealand. Extinction was not concentrated during a few critical periods, but was rather well-distributed during the entire Cenozoic. By contrast, the data available to the writer, through literature and discussion with colleagues, indicate that perhaps no more than seven genera and subgenera out of not less than 300 Tethyan immigrants, became extinct in the Cenozoic of Japan. These taxa and their times of extinction are: Eocene - *Crassatellites* (*Eucrassatella*), *Venericardia* (*Venericor*), *Lima* (*Meotolima*); Oligocene - *Venericardia* (*Venericardia*), *Claibornites*, *Hubertschenkia*; Miocene - *Vicarya*. This apparently marked difference in extinction histories would seem to indicate that the Tethyan immigrants of New Zealand were subject to rather high levels of adaptive stress throughout the Cenozoic whereas in Japan conditions seem to have been equable for all elements present (Tethyan, North Pacific, and Mesozoic holdovers) and well within the adaptive capability of the bivalve and gastropod genera there.

A number of factors suggest that New Zealand was indeed subjected to significantly changing environments during the full span of the Cenozoic (KENNETT, HOUTZ, ANDREWS *et al.*, 1974). These include (1) the persistent northward drift of New Zealand of some 1000-1300 km between the Eocene and Recent. [During the same interval, Japan apparently remained at essentially the same latitudinal position (DIETZ & HOLDEN, 1970)] (2) Exposure of New Zealand to the cold circum-Antarctic current beginning in the Oligocene, caused by a progressively enlarging strait between a northward-drifting Australia and Antarctica, and (3) progressive alteration and interference of southeast-flowing Indo-Pacific equatorial currents carrying Tethyan molluscan larva to New Zealand by the northward-drifting Australia. Antarctic glacial episodes in the Eocene, Oligocene, late Miocene, Pliocene, and Pleis-

tocene (KENNETT, BURNS, ANDREWS *et al.*, 1972; SHACKLETON & KENNETT, 1975) also would be expected to have persistently affected the marine conditions in New Zealand. The New Zealand and Japanese histories sketched above, though reflecting some differences in detail, would seem to point up the growing importance of the effects of plate movements, paleo-current circulations and paleographic settings, in addition to more local events, in interpreting the biogeographic history of marine organisms.

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Review of the Bivalve Genus *Pholadomya* from the Tertiary of California and the Description of Two New Species

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(1 Plate)

THE GENUS *Pholadomya* is a common member of Mesozoic and early Cenozoic molluscan faunas, but becomes rare in later Cenozoic and Recent faunas. Detailed systematic study of fossil members of the genus is very difficult because of the generalized shell morphology and the thin shell is rarely preserved. Most fossil species of *Pholadomya* are known only from molds and casts.

Pholadomya is characterized by a small to medium sized, ovate to subtrigonal, thin-walled nacreous shell. The genus is strongly inequilateral with broadly rounded to subangular umbones located near the anterior margin of the shell. The ornamentation consists of prominent concentric undulations of varying strength. The anterior two thirds of the shell is generally decorated with narrow radial ribs which may or may not reach the ventral margin. The intersection of the radial and concentric ornamentation frequently results in the formation of low rounded nodes. Small delicate pustules cover the entire surface of the shell, but are only rarely preserved on fossil materials. The posterior gape is well developed, but varies considerably in width. The Recent type species (*P. candida* Sowerby) has a very weak hinge with a single obsolete tooth supported by a vertical buttress-like ridge below the beak in each valve (RUNNEGAR, 1972). The presence of a shallow depression in the hinge of each valve led Waterhouse to speculate that the depression was a ligamental pit. RUNNEGAR (1972) questioned Waterhouse's interpretation, but did not put forth any alternative function for the pits in the hinge plate.

Little is known about the ecology and life habits of the family Pholadomyidae. All Recent members of the family are rare, and most are restricted to deep water of the subantarctic region. Although exceedingly rare, *P. candida* Sowerby occurs in warm shallow waters of the West Indies

(RUNNEGAR, 1972). Most of the California species appear to have lived in fairly deep water, but the occurrence of *P. nasuta* Gabb with shallow water assemblages in the Simi Hills indicates that the genus was not restricted exclusively to deep water habitats during the Tertiary. An examination of the shell morphology provides a number of clues to the ecologic requirements of the genus.

The thin elliptical, bluntly elongated shell with an extremely weak hinge is characteristic of a deep burrowing bivalve in a firm stable substrate (STANLEY, 1970). *Pholadomya* probably lives in a permanent burrow with an open siphonal tube to the surface. The general occurrence of fossil species in fine sandy siltstones with articulated valves supports this type of habitat.

The cosmopolitan genus *Pholadomya* first appeared in the Late Triassic and has survived to the Recent. Although a number of Recent species have been referred to *Pholadomya*, only *P. candida* Sowerby resembles the fossil forms. The other Recent small pholadomya-like bivalves, mainly from antarctic and subantarctic waters, probably belong to the genus *Panacca* Dall, 1905 or should be placed within a new genus.

The purpose of this note is to review the Tertiary species of *Pholadomya* from California. Except for the Paleocene species (*P. nasuta* Gabb), the genus is rare. In the Paleocene, the genus is represented by two species. *P. nasuta* Gabb is moderately abundant and occurs throughout the Paleocene. The other Paleocene species of pholadomyid (*P. mouni* n. sp.) is rare and known only from a single specimen collected by Charles E. Weaver from the basal Lodo Formation, Fresno County and 7 specimens from the "Martinez marine member" of the lower part of the Santa Susana Formation from the Simi Hills. Two species are known to occur in the Eocene. *P. givensi* n. sp. occurs in

the lower Middle Eocene Juncal Formation near Pine Mountain, Ventura County and *P. murrayensis* Hanna is known from a single specimen from the upper Middle Eocene of Rose Canyon, San Diego County. The only other known occurrence of the genus is *P. kernensis* Wiedey from the Middle Miocene Temblor Formation, Kern County.

COOPER (1896) in a short paper describing several new fossil mollusks from California referred a coarsely ribbed species from the Eocene to the genus *Pholadomya*. He further proposed a new subgenus (*Triplicosta*) based on this species. COX & NEWELL (1969) questionably raised *Triplicosta* to generic rank in the Treatise. The radial sculpture of *P. (T.) progressiva* Cooper is not typical of the ornamentation of the Pholadomyidae. Instead of becoming obsolete on the dorsal posterior quarter of the shell, the ribs become progressively stronger. The relatively thick non-nacreous shell together with radial ornamentation indicates as Cooper suggested that *P. (T.) progressiva* Cooper probably does not belong to the Pholadomyidae, but to some veneroid such as *Cardita* or *Petricola*.

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Institute of Polar Studies Miscellaneous Contribution No. 121.

The following abbreviations are used in the text:
A.N.S.P.: Academy of Natural Sciences, Philadelphia
U.C.M.P.: University of California Museum of Invertebrate Paleontology, Berkeley
U.C.R.: University of California, Riverside
L.S.J.U.: Leland Stanford Junior University

SYSTEMATIC PALEONTOLOGY

BIVALVIA

Pholadomyoidea

PHOLADOMYACEA

Pholadomyidae

Pholadomya Sowerby, 1823

Type: (by SD) *Pholadomya candida* Sowerby (*Pholadomya*) Sowerby, 1823, sensu stricto.

Subrectangular to ovate, umbones broad, low, located approximately one-eighth to one-quarter the length of shell from anterior margin; dorsal umbonal ridge present; es-cutcheon present or absent.

Geologic Range: Upper Triassic to Recent.

Pholadomya (Pholadomya) nasuta Gabb, 1864

(Figure 5)

Pholadomya nasuta Gabb, 1864; 1: 152; pl. 30, fig. 124; STANTON, 1896: 1024; WEAVER, 1905: 116-117; pl. 12, fig. 6; DICKERSON, 1914: 108, 151; pl. 9, figs. 1a, 1b; McLAUGHLIN & WARING, 1915: fig. 13; WARING, 1917: 72; pl. 12, fig. 17; CLARK, 1929: pl. 1, figs. 2, 7; STEWART, 1930: 301, 302; pl. 7, fig. 7; SCHENCK & KEEN, 1940: pl. 19, fig. 1.

Holotype: A.N.S.P. no. 4562

Type locality: "On the shore of the Straits of Carquines, 2 miles west of Martinez" (GABB, 1864).

Geographic distribution: Throughout the Paleocene of California.

Geologic range: Upper Paleocene. In the Simi Hills, it occurs within the planktonic foraminifera *Globorotalia pseudomenardii* (P₄) zone (ZINSMEISTER, 1975).

Discussion: This common species of *Pholadomya* is easily separated from other Paleocene pholadomyas of California by its large subrectangular outline and low rounded umbones. The posterior dorsal margin is only slightly concave. *Pholadomya (P.) murrayensis* Hanna also has a subrectangular outline, but the beaks are more centrally located and the posterior dorsal margin is distinctly concave. The ventral margin of *P. (P.) murrayensis* is not as broadly rounded.

Pholadomya (Pholadomya) murrayensis Hanna, 1927

(Figure 2)

Pholadomya murrayensis Hanna, 1927: 279; pl. 33, figs. 12, 13.

Holotype: U.C.M.P. no. 31150

Type locality: U.C.M.P. loc. 4229, elevation 325 feet at south side of road 0.19 inches west of the top of the "3" of B.M. 394, (La Jolla Quad.), north of Mission Valley, San Diego County, California (HANNA, 1927).

Geographic distribution: Known only from type locality.

Geologic range: upper Middle Eocene "Tejon Stage"

Discussion: This small distinctive species of *Pholadomya* from the late Middle Eocene has a more centrally located beak than either *P. (P.) nasuta* Gabb or *P. (P.) kernensis* Wiedey. The strong rectangular outline of the shell is not immediately apparent because the ventral margin is slightly crushed. The radial sculpture of *P. (P.) murrayensis* Hanna extends to the ventral margin and covers the anterior two thirds of the shell.

Pholadomya (Pholadomya) kernensis Wiedey, 1928

(Figure 4)

Pholadomya kernensis Wiedey, 1928: 141-142; plt. 17, figs. 1, 2.

Holotype: L.S.J.U. no. 437, (Stanford's molluscan collections have been transferred to the California Academy of Sciences, San Francisco).

Type locality: L.S.J.U. loc. 438, SW 1/4 of SE 1/4 of Section 12, T. 275., R. 28 E., north of Poso Creek, Kern County, California (WIEDEY, 1928).

Geographic distribution: Known only from type locality.

Geologic range: Middle Miocene, Temblor Formation.

Discussion: *Pholadomya (P.) kernensis* Wiedey is similar in size to *P. (P.) nasuta* Gabb, but may be distinguished by its slightly more elongated outline, narrower anterior margin, sharper beak, and a wider gape. The radial ribs are fewer in number and tend to become obsolete near the ventral margin. Posterior to the central radial ribs on *P. (P.) kernensis* Wiedey are 3 to 4 narrow widely spaced continuous ribs.

(*Bucardiomya*) Rollier in Cossman, 1912

Type: (by SD) *Pholadomya bucardium* Agassiz.

Subtrigonal to obliquely oval, umbones high, prominent, subangular, located near anterior margin, escutcheon absent.

Geologic range: Lower Jurassic to Lower Tertiary.

Pholadomya (Bucardiomya) mounti Zinsmeister, spec. nov.

(Figures 3, 6, 7)

Description: Shell thin walled, moderately inflated, subtrigonal, markedly inequilateral. Beaks elevated, subangular, located near anterior margin. Posterior dorsal margin slightly to moderately concave; anterior margin nearly straight; posterior and ventral margin broadly rounded. Sculpture - numerous well developed irregularly spaced concentric undulations; radial ribs (6 to 12) extend to ventral margin, restricted to anterior two thirds of shell; small blunt nodes formed by intersection of radial ribs and concentric undulations.

Dimensions: Holotype no. U.C.R. 6898/101, length 46 mm; height 40 mm; Paratype U.C.R. no. 6899/4, length 30 mm, height 28 mm; Paratype U.C.R. no. 6898/102, length 36 mm (incomplete), height 49 mm.

Type locality: U.C.R. loc. 6898, medium brown, fine grained sandy siltstone at bottom of steep road cut, 2 790 feet 34° SW of hill 1331; 3 675 feet 11° SE of SW corner of Section 14, T. 2 N., R. 18 W. (ZINSMEISTER, 1974).

Geographic distribution: Fresno County south to Ventura County, California.

Geologic range: Paleocene.

Discussion: *Pholadomya (Bucardiomya) mounti* is distinguished from *P. (B.) givensi* by its large size, concave posterior margin and broadly rounded anterior margin. The radial ribs of *P. (B.) mounti* extend to the ventral margin while those of *P. (B.) givensi* tend to become obsolete.

Explanation of Figures 1 to 7

Figure 1: *Pholadomya (Bucardiomya) givensi* Zinsmeister, spec. nov. Holotype U.C.R. 4662/110; lower Middle Eocene, Pine Mountain, Ventura County, California X 1

Figure 2: *Pholadomya (Pholadomya) murrayensis* Hanna, Holotype U.C.M.P. 31150, upper Middle Eocene, San Diego County, California X 1.5

Figure 3: *Pholadomya (Bucardiomya) mounti* Zinsmeister, spec. nov. Paratype U.C.R. 6899/4; Upper Paleocene, Simi Hills, Ventura County, California X 1

Figure 4: *Pholadomya (Pholadomya) kernensis* Wiedey. Holotype L.S.J.U. 437, north of Poso Creek, Kern County, California X 1
Figure 5: *Pholadomya (Pholadomya) nasuta* Gabb. Hypotype, U.C.R. 6813/4; Upper Paleocene, Simi Hills, Ventura County, California X 1

Figure 6: *Pholadomya (Bucardiomya) mounti* Zinsmeister, spec. nov. Paratype U.C.R. 6898/102; Upper Paleocene, Simi Hills, Ventura County, California X 1

Figure 7: *Pholadomya (Bucardiomya) mounti* Zinsmeister, spec. nov. Holotype U.C.R. 6898/101; Upper Paleocene, Simi Hills, Ventura County California X 1



Figure 1



Figure 2

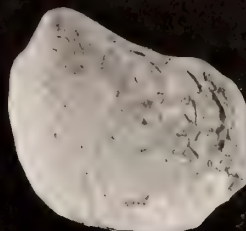


Figure 3

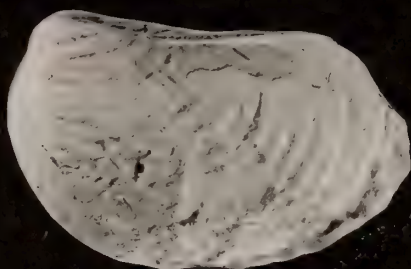


Figure 4



Figure 5

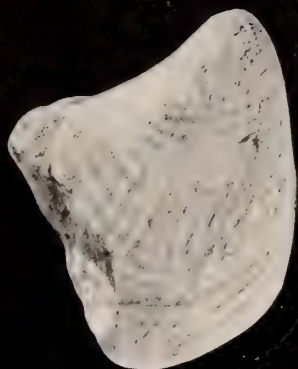


Figure 6

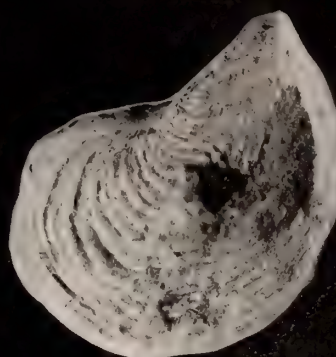


Figure 7



The high subangular beak separates it from the *Pholadomya* s. s. group from other pholadomyas. Occasionally, some individuals of *P. (B.) mounti* will develop a more rounded anterior margin, but they never attain the subrectangular outline of *P. (P.) nasuta* Gabb.

This species of *Pholadomya* is named for Jack D. Mount at the University of California, Riverside.

Pholadomya (Bucardiomya) givensi Zinsmeister, spec. nov.

(Figure 1)

Pholadomya (Pholadomya) sp. Givens, 1974: 58; plt. 4, fig. 5.

Description: Shell thin-walled, inflated, elongate to sub-trigonal, equivalve, strongly inequilateral. Beaks high, subangular, located near anterior margin; gape narrow; posterior dorsal margin slightly concave to nearly straight, posterior and ventral margin broadly rounded, anterior margin nearly straight. Sculpture - concentric undulation of variable width and strength; radial ribs (12 to 15) weakly tuberculated, restricted to central part of shell, become obsolete near mid-point of shell.

Dimensions: Holotype U.C.R. no. 4662/110, length 33 mm; height 22 mm.

Type locality: U.C.R. loc. 4662; "In bed of Hot Spring Canyon 2,450 ft. N., 2,050 ft. W. of SE cor. Sec. 21, T. 6 N., R. 20 W, Topatopa Mountain Quad." (GIVENS, 1974).

Geographic distribution: Known only from type locality.

Geologic range: Lower Middle Eocene.

Discussion: *Pholadomya (Bucardiomya) givensi* is distinguished from *P. (B.) mounti* by its relatively straight posterior dorsal margin, failure of the radial to reach ventral margin, and extreme anteriorly located beaks. The shell of *P. (B.) mounti* is considerably larger and more inflated.

Pholadomya (B.) givensi is known only from 8 specimens. Only the holotype is well preserved, the remaining individuals are crushed. The anterior location of the beak and other morphologic similarities of the two species suggest that the lower Middle Eocene *P. (B.) givensi* is probably a lineal descendant of *P. (B.) mounti*.

This species of *Pholadomya* is named in honor of Dr. C. R. Givens.

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The Chromodoridinae Nudibranchs from the Pacific Coast of America. - Part IV. The Genus *Hypselodoris*

BY

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(1 Plate; Text figures 26 to 32)

THIS PAPER IS THE FOURTH and concluding part of The Chromodoridinae Nudibranchs from the Pacific Coast of America. Previous segments have discussed various techniques and criteria for opisthobranch systematics, and supra-specific taxonomy of the CHROMODORIDIDAE (BERTSCH, 1977), and known species of the genera *Chromodoris* (BERTSCH, 1978a), *Chromolaichma* and *Mexichromis* (BERTSCH, 1978b).

Hypselodoris Stimpson, 1855*Hypselodoris agassizii* (Bergh, 1894)

(Figures 3-L, 26, 29 - 32)

References and Synonymy:

- Chromodoris agassizii* BERGH, 1894: 182-183; plt. 7, figs. 14-22. BERGH, 1898: 533. BERGH, 1905a: 71. COCKERELL & ELIOT, 1905: 36. BERGH, 1905b: 156. MACFARLAND, 1906: 129. BERTSCH, 1970: 7.
- Glossodoris agassizi* (Bergh). PRUVOT-FOL, 1951a: 78-79. ABBOTT, 1974: 355, fig. 4250 [first figure so numbered, bottom left hand side of the page]
- Hypselodoris agassizi* (Bergh). SPHON, 1971: 214. SPHON & MULLINER, 1972: 150-151. MARCUS & HUGHES, 1974: 520.
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- Glossodoris aegialia* (Bergh). PRUVOT-FOL, 1951a: 78. ABBOTT, 1974: 355.

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Editor's Note: For Figures 3-A, 3-B, etc. see The Veliger 20 (2): 115

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- Hypselodoris californiensis* (not Bergh, 1879). MARCUS & MARCUS, 1967: 176-178 (in part); fig. 31 (locality 2). MARCUS, 1971: 357 (in part). KEEN, 1971: 823 (in part); fig. 2335. BRUSCA, 1973: 174 (in part); fig. 6.68.
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Material Examined and Distribution:**Baja California, Mexico:**

- 1) 1 specimen, Isla Espíritu Santo (24°25'N; 110°21'W); leg. A. J. Ferreira, 27 November 1973 (HB 367)
- 2) 1 specimen, La Paz area; leg. E. Janss Jr., no date

Mainland Mexico and Central America:

- 3) 2 specimens, Puerto Peñasco, Sonora; leg. G. E. & N. MacGinitie, 23-27 December 1948 (HB 439 A-B; CAS)
- 4) 1 specimen, Cabo Tepoca, Punta Lobos, Sonora; leg. F. & R. Poorman, March 1975 (HB 426; LACM A 8477)
- 5) 1 specimen, Bahía San Carlos, Sonora; leg. A. J. Ferreira, August 1972
- 6) 1 specimen, Morro Colorado, near Guaymas; leg. A. Kerstitch, May, 1972
- 7) 6 specimens, La Cruz, Nayarit; leg. F. & R. Poorman, 3 January 1976 (HB 417 A-F; LACM A 8477)
- 8) 5 specimens, intertidal, Bahía Banderas, Jalisco; leg. H. DuShane, 24 February 1971 (HB 387 A-E; LACM A 8530)
- 9) 2 specimens, Isla Pajaro, Panama; leg. P. W. Glynn, 21 May 1972 (HB 264 A-B)

- 10) 1 specimen, Contadora Island, Panama; leg. A. F. Ferreira, February 1975 (HB 368)
 11) 1 specimen, intertidal, Culebra Island, Balboa, Panama; leg. H. Bertsch & K. B. Meyer, 7 August 1974 (HB 132)
 12) 1 specimen, subtidal, Taboguilla Island, Panama; leg. G. Hendler, 30 August 1974 (HB 192)
 13) 1 specimen, Taboguilla Island, Panama; leg. G. Hendler, 30 August 1974 (HB 193)
 14) 1 specimen, Taboguilla Island, Panama; leg. G. Hendler, 6 September 1974 (HB 205)
 15) 1 specimen, Taboguilla Island, Panama; leg. G. Hendler, 11 September 1974 (HB 219)
 16) 1 specimen, Culebra Island, Panama; leg. H. Bertsch & K. B. Meyer, 17 September 1974 (HB 221)
 17) 1 specimen, Culebra Island, Panama; leg. H. Bertsch & K. B. Meyer, 17 September 1974 (HB 222)

South America:

- 18) 1 specimen, Academy Bay, Santa Cruz Island, Galápagos Islands; leg. A. G. Smith, February 1964

Published records of the occurrence of *Hypselodoris agassizii* are the Gulf of California from mainland, Sonora, Mexico (Puerto Peñasco, Cabo Tepoca, Puerto Libertad, and Guaymas) and Baja California (Salatito Bay and Pulmo Reef), from southern Mexico (Sayulita, Nayarit; and Bahía Banderas, Jalisco), Central America (Bahía Ballenas, Costa Rica; and the type locality, Panama Bay, Panama), and one specimen from the Galápagos Islands (FERREIRA & BERTSCH, 1975: 327).

WHITE (1952: 116 - 118; fig. 16) reported a specimen from Florida as *Glossodoris aegialia*. This is erroneous; the specimen was probably *Hypselodoris edenticulata* (White, 1952).

External Morphology and Coloration:

Living specimens from Panama ranged from 18 - 29 mm in total length ($\bar{X} = 21.8$ mm, $n = 6$). Body color is dark blue. On the notum and lateral and posterior sur-

Table 13

Radular Variation in *Hypselodoris agassizii*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row	Maximum number of smooth teeth per half-row
1	—	—	—	65	105	—
2	—	—	—	51	85	—
205	2.44	1.64	1:1.49	68	92	72
219	2.53	1.43	1:1.77	58	73	0
221	1.43	0.91	1:1.57	47	56	—
222	1.52	1.05	1:1.45	52	64	—
264 A	2.87	2.28	1:1.26	71	103	92
264 B	4.69	3.39	1:1.38	80	110	—
367	1.19	0.79	1:1.51	48	50	—
368	4.34	3.54	1:1.23	80	118	96
387 B	3.84	2.77	1:1.39	71	117	95
387 C	3.47	2.38	1:1.46	69	100	87
387 D	4.12	2.81	1:1.47	76	110	93
387 E	3.17	2.32	1:1.37	64	92	79
417 A	3.05	2.3	1:1.33	66	118	90
417 B	3.35	2.24	1:1.5	66	113	94
417 C	2.24	1.62	1:1.38	58	95	77
417 D	1.818	1.212	1:1.5	56	80	45
417 E	2.53	1.37	1:1.85	61	94	68
417 F	2.44	1.78	1:1.37	65	87	69
426	2.83	2.28	1:1.24	69	96	73
439 A	2.77	2.04	1:1.36	66	79	58
439 B	4.24	3.03	1:1.4	72	102	85
\bar{X}	2.89	2.056	1:1.44	64.3	93	74.88
s	0.984	0.785	0.153	9.29	19.2	23.99

¹BERGH, 1894; ²MARCUS & MARCUS, 1967.

faces of the foot are numerous small yellow (or orangish) dots. At times there are also elongate, ovalish white marks on the notum; one specimen from Panama had 2 longitudinal rows of the white marks (each with 2 spots on the anterior half of the dorsum, and 3 spots on the posterior half of the dorsum in front of the gills). BERGH (1894: 182) described this variation (of larger white streaks) in the original description of *Hypselodoris agassizii*, although he was using preserved material in which the yellow had faded: "...überall am Rücken und an den Seiten eine Menge von kleinen ovalen weissen Punkten oder Fleckchen vorkam, welche hier und da durch Verschmelzen kurze Striche und einzelne Flecken bildeten." The amount and size of the white streaks vary in different animals; MARCUS & MARCUS (1967: 177; fig. 31) studied a specimen which had only 1 white streak posterior to the right rhinophore.

Surrounding the mantle edge are 3 colored stripes; a light green one innermost, a yellow band on the outside, and a navy blue or black band between. These stripes are broken anteriorly (in front of the rhinophores) and laterally (approximately in the middle of the animal's length). Rhinophores are dark blue, with small yellowish

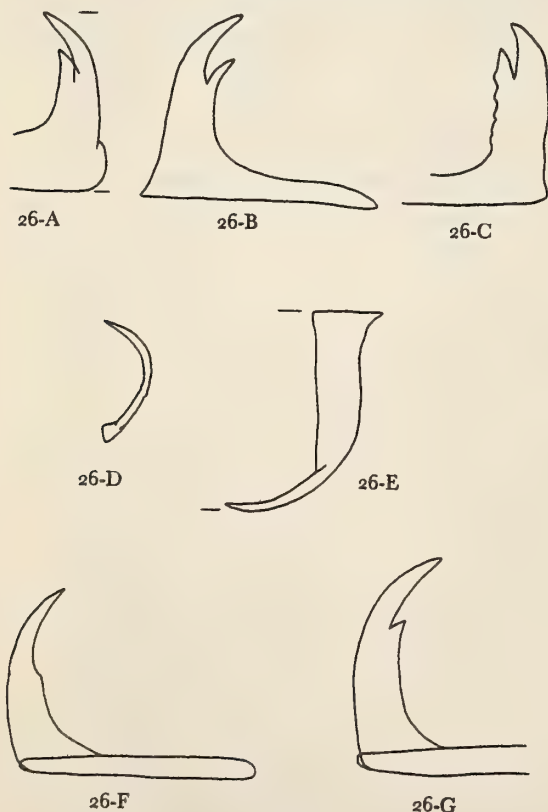


Figure 26

Radular teeth of *Hypselodoris agassizii*

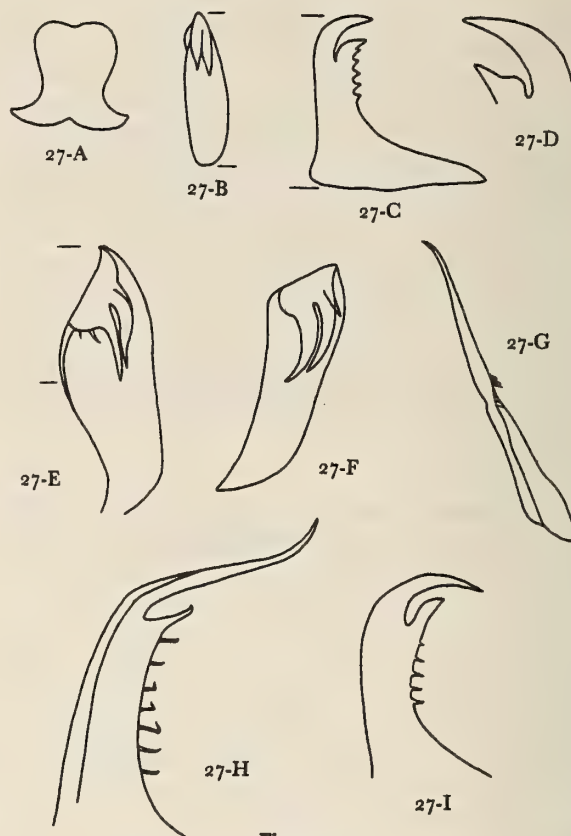


Figure 27

Radular teeth of *Hypselodoris californiensis*

- A - HB 360; outline sketch of radula mounted flat
- B - HB 406; 1st lateral tooth, row 26, RSR; LBM, 0.038 mm
- C - HB 406; tooth 69, row 26, RSR; LBM, 0.06 mm; length of base, 0.06 mm
- D - HB 407; distal shaft, 2 main cusps of an inner lateral tooth
- E - HB 360; developing innermost tooth, row 68 (penultimate), LSR; LBM, 0.026 mm
- F - HB 360; developing innermost tooth, row 66, LSR
- G - HB 407; developing outermost lateral tooth, row 87 (ultimate), LSR; total length, 0.093 mm
- H - HB 407; developing inner lateral tooth, row 87 (ultimate), LSR
- I - HB 252 C; nearly fully-formed lateral tooth (inner $\frac{1}{4}$ of half-row), row 52, LSR

(← adjacent column)

- A - HB 439 A; smooth inner lateral, tooth 28, row 28, LSR; LBM, 0.09 mm
- B - HB 387 B; smooth inner lateral, tooth 84, row 21, LSR
- C - HB 387 D; denticled outer lateral tooth, row 31, RSR
- D - HB 387 C; developing lateral tooth, row 69 (ultimate); LBM, 0.03 mm
- E - HB 387 D; developing lateral tooth, row 67, LSR; LBM, 0.08 mm
- F - HB 387 D; developing lateral tooth, row 60, LSR; LBM 0.073 mm; length of base, 0.105 mm
- G - HB 387 D; developing lateral tooth, row 59, LSR; LBM, 0.078 mm

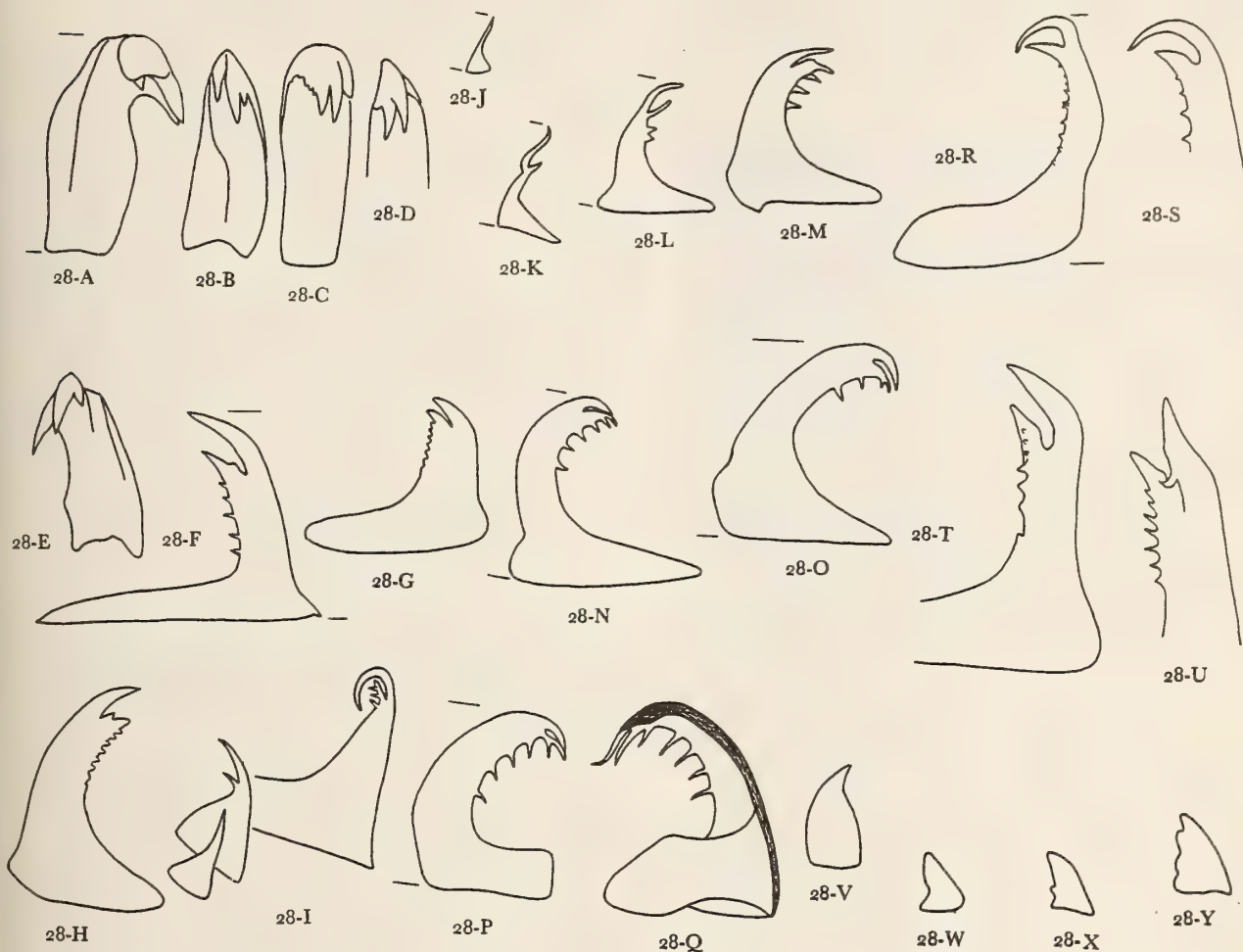


Figure 28

Radular teeth of *Hypselodoris ghiselini*

- A - HB 86 A; innermost lateral tooth, row 20, RSR; LBM, 0.065 mm; a ridge (or flange) is visible along the left (inner) side of the base; the bicuspid tip and the denticle on the distal inner surface of the shaft are also shown
- B - HB 318 D; innermost lateral tooth, row 28, LSR
- C - HB 318 B; innermost lateral tooth, row 29, LSR
- D - HB 428 A; innermost lateral tooth, row 38, LSR
- E - HB 428 A; innermost lateral tooth, row 37, LSR; LBM, 0.054 mm; visible are the bicuspid tip and denticle on inner surface (upper left of figure), and the lengthwise basal flange (right side of figure)
- F - HB 26; representative lateral tooth from middle of half-row; LBM, 0.074 mm; length (measured from base of notch between 1st and 2nd cusps to cusp tip) of primary cusp is 0.028 mm, and of secondary cusp is 0.018 mm; base of tooth 0.097 mm
- G - HB 318 B; isolated lateral tooth from anterior portion of radula

- H - HB 89; lateral tooth from middle of half-row, approximately row 27, RSR
- I - HB 318 D (USNM 753567); developing teeth in 3 successive rows (drawn in relative proportion and position); smallest tooth is 3rd newest row of radula, largest is 5th
- J - Q - HB 318 C; sequence of developing teeth, last row, from center of radula to outer edge
- J - LBM, 0.019 mm
- K - LBM, 0.042 mm
- L - LBM, 0.038 mm (curvature of shaft increases; measurement made to greatest height, not along entire shaft, and hence this tooth is shorter than the younger tooth figured in 28K)
- M - LBM, 0.048 mm
- N - LBM, 0.034 mm
- O - LBM, 0.044 mm
- P - LBM, 0.044 mm
- Q - Tooth is thickened along the anterior ridge
- R - U - HB 86-B; sequence of developing lateral teeth from center of half-rows
- V - HB 100 A; jaw platelet; 0.024 mm long
- W - Y - HB 87; jaw platelets; all approximately the same size, 0.01 mm high, 0.008 mm wide

flecks. Gills are white basally, with the distal tips dark blue.

Radula:

Meristic characters of 23 radulae (including the reported data from 2 radulae by BERGH, 1894, and MARCUS & MARCUS, 1967) are in Table 13. The data reported for *Chromodoris aegialia* BERGH (1905a: 71) were not used for the calculation of means nor regression lines. The combined radular formula is 47-80 (50-118·0·50-118) (including *C. aegialia*, the known maximum number of tooth rows is 85).

The number of tooth rows and maximum number of teeth per half-row are positively correlated (Figure 29). The regression line formula is $Y = -18.01 + 1.726 X$; $r = 0.8349$, $P < 0.001$, $n = 23$.

The number of tooth rows is dependent on the length of the radula (Figure 30). The equation for the regression line is $Y = 39.57 + 8.74 X$. The coefficient of correlation is 0.9295 ($P < 0.001$, $n = 21$).

The maximum number of teeth per half-row is positively correlated with the radular width (Figure 31).

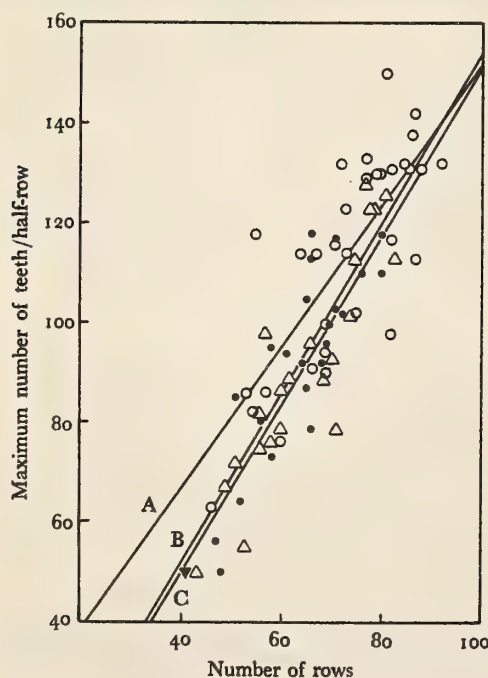


Figure 29

Correlation between maximum number of teeth per half-row and number of tooth rows. A - *Hypselodoris agassizii* (dots); B - *H. californiensis* (○); C - *H. ghiselini* (△); and *H. lapislazuli* (▲)

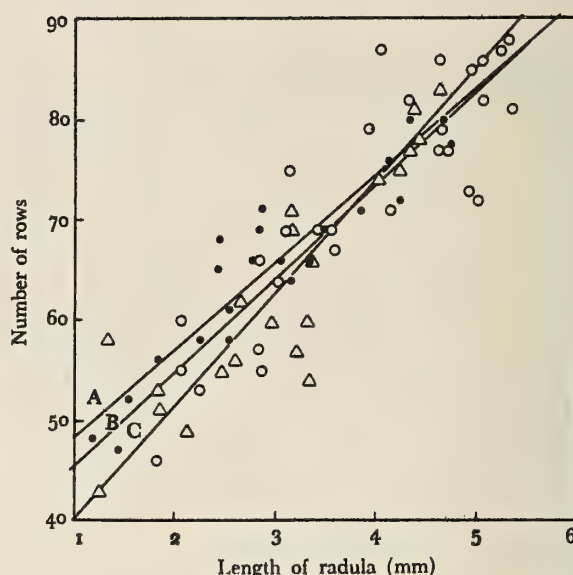


Figure 30

Relation between number of rows and length of radula, *Hypselodoris agassizii*, *H. californiensis*, and *H. ghiselini*. Symbols as in Figure 29

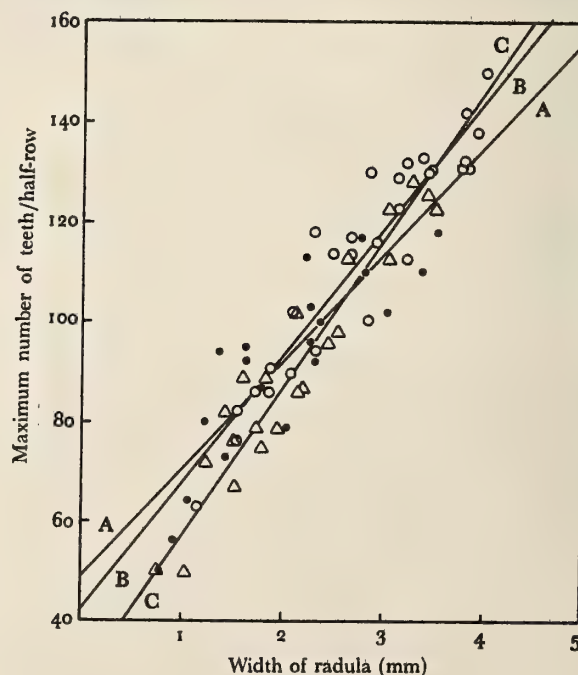


Figure 31

Correlation between maximum number of teeth per half-row and width of radula, *Hypselodoris agassizii*, *H. californiensis*, and *H. ghiselini*. Symbols as in Figure 29

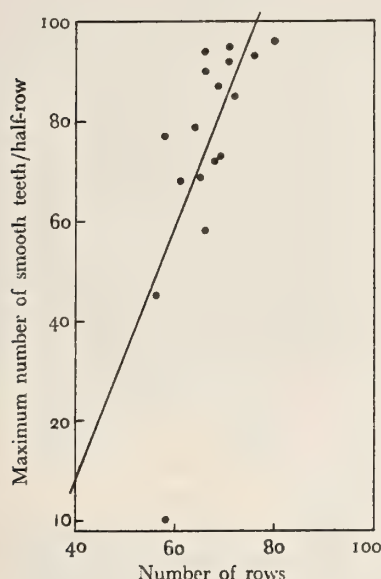


Figure 32

Correlation between maximum number of smooth teeth per half-row and number of tooth rows, *Hypselodoris agassizii*

The formula, $Y = 48.84 + 21.38 X$, describes the regression line ($r = 0.8439$, $P < 0.001$, $n = 21$).

The maximum number of smooth (without denticles) lateral teeth per half-row is dependent on the number of rows (Figure 32). The regression line formula is $Y = -95.82 + 2.55 X$ ($r = 0.6786$, $P < 0.01$, $n = 17$).

Radular teeth are bicuspid (FERREIRA & BERTSCH, 1975: figs. 7-8, scanning electron micrographs of the lateral teeth). The inner lateral teeth have no denticles (Figure 26 A-B), but outermost teeth are denticled (Figure 26 C). The number of smooth teeth is a function of the size of the radula. The smooth lateral teeth were noted by BERGH (1894: 183), but overlooked in recent works (MARCUS & MARCUS, 1967: 178; SPHON, 1971: 214). This is an important characteristic; and even considering the ontogenetic change of this quality, it clearly separates *Hypselodoris agassizii* from *H. californiensis*, *H. ghiselini*, and *H. lapislazuli*.

Stages of development of the smooth lateral teeth are shown in Figure 26 D-G. The tooth begins as a small, curled, sickle-shaped, pointed hook, then thickens and elongates, as the primary cusp becomes prominent. The secondary cusp is initially a small point, which lengthens as the entire tooth becomes larger.

Discussion:

Chromodoris aegialia was described in 1904 from a single preserved specimen collected in the Gulf of Califor-

nia. It has remained an enigmatic species since that original description, included for completeness in taxonomic and faunal lists only as a reference to Bergh's report.

Based on the known range of color variation of *Hypselodoris agassizii*, its radular morphology and the regression analyses of its meristic qualities, I conclude that *Chromodoris aegialia* is a junior subjective synonym of *Hypselodoris agassizii*.

BERGH (1905a: 70-71) describes *Chromodoris aegialia* as greenish-white, with various rows of white streaks and dots, 4 small white bands around the mantle border, and 2-3 lengthwise rows of short white streaks and flecks. Living *Hypselodoris agassizii* has a dark blue notal center, with rows of yellow streaks and dots, and usually 3 colored bands around the mantle border, and 3 or 4 irregular rows of yellow spots on the sides of the foot. The overall impression of the two is similar; differences are attributable to preservation artifacts. There is no compelling reason to consider the coloration different.

The probable similarity of the species seen by their external coloration, is made definitive by an examination of the radula. The specimen named *Chromodoris aegialia* has bicuspid lateral teeth, with no denticles. All the lateral teeth are smooth. The radular formula Bergh gives is 85 (110 · 0 · 110). The number of smooth lateral teeth of *Hypselodoris agassizii* increases with the larger number of tooth rows (Figure 32). Plotting the number of tooth rows of *C. aegialia* results in a point adjacent to the calculated regression line of *H. agassizii* (the line crosses 80 rows at 110 smooth teeth per half-row), well within the expected (and statistically derived) range of variation for *H. agassizii*. The specimen that Bergh described as *C. aegialia* is simply a large *H. agassizii* in which all the lateral teeth are without denticulation.

Hypselodoris californiensis (Bergh, 1879)

(Figures 3-M, 27, 29-31, 61-64)

References and Synonymy:

- Chromodoris californiensis* BERGH, 1879c: 72, 109, 112-114. BERGH, 1884: 649. ORCUTT, 1885: 545. BERGH, 1890a: 168; plt. 3, fig. 14. BERGH, 1890b: 940. BERGH, 1891: 141. BERGH, 1892: 118. BERGH, 1898: 533. BERGH, 1905a: 71. COCKERELL & ELIOT, 1905: 36, 37-38. BERGH, 1905b: 156. MACFARLAND, 1906: 129-130. COCKERELL, 1908: 106. JOHNSON & SNOOK, 1927: 494, plt. 9, fig. 4. MACGINITIE & MACGINITIE, 1949: 379. MACFARLAND, 1966: 157-162; plt. 24, figs. 1-3; plt. 34, figs. 12-23. RUSSELL, 1968: 140-141. BLOOM, 1976: 293, 294.
- Chromodoris calensis* BERGH, 1879a: 3. BERGH, 1879b: 103. BERGH, 1880: 125, plt. 14, figs. 5-15.
- Chromodoris glauca* BERGH, 1879b: 88, 103, 106-107. BERGH, 1879a: 3 (*nomen nudum*). BERGH, 1879c: 109. BERGH, 1884: 649. BERGH, 1890a: 168. BERGH, 1890b: 940.

- BERGH, 1891: 141. BERGH, 1892: 118. BERGH, 1905b: 156.
- Glossodoris glauca* (Bergh). PRUVOT-FOL, 1951a: 106.
- Chromodoris universitatis* COCKERELL, 1901: 79. COCKERELL, 1902: 19-20. COCKERELL & ELIOT, 1905: 36, 37-38. MACFARLAND, 1906: 129-130.
- Glossodoris universitatis* (Cockerell). PRUVOT-FOL, 1951a: 90. PRUVOT-FOL, 1951b: 152. ABBOTT, 1974: 355.
- Chromodoris* sp. GUERNSEY, 1912: 75; figs. 39 C-D.
- Glossodoris californiensis* (Bergh). O'DONOGHUE, 1926: 211. O'DONOGHUE, 1927: 90-91; plt. 2, figs. 38-42. SMITH & GORDON, 1948: 180. PRUVOT-FOL, 1951a: 89-90. PRUVOT-FOL, 1951b: 152. WHITE, 1952: 114. STEINBERG, 1961: 62. LANCE, 1961: 66. PAINE, 1963: 4, 8. FARMER & COLLIER, 1963: 62. STEINBERG, 1963: 69. LANCE, 1966: 69, 70, 72 (may be only in part). FARMER, 1967: 341. SPHON & LANCE, 1968: 79. RICKETTS & CALVIN, 1968: 119, 514. ABBOTT, 1974: 355 (in part); fig. 4250 (second illustration with that number, upper right hand quarter of the page).
- Hypselodoris californiensis* (Bergh). MARCUS & MARCUS, 1967: 59, 176-178 (in part; not any of the material examined nor figures), 238. FARMER, 1968: 24-25. ROLLER & LONG, 1969: 425-429. ROLLER, 1970a: 371. LONG, 1970: 19. MCBETH, 1971a: 28. KEEN, 1971: 823 (in part, not fig. 2335); plt. 20, fig. 1. MCBETH, 1971b: 158. SPHON, 1971: 214 (in part). FARMER, 1971: 19. SPHON & MULLINER, 1972: 150. SPHON, 1972b: 65. BERTSCH *et al.*, 1973: 287. BERTSCH, 1973: 109. BRUSCA, 1973: 174 (in part; not fig. 6.68). FERREIRA & BERTSCH, 1975: 326-327. KEEN & COAN, 1975: 44. SMITH & CARLTON, 1975: 528, 540.

Bergh had intended the species name to be *calensis*, but the typesetter changed it in the text to *californiensis*; since the text was printed before the plate (on which *calensis* remained unaltered), the name *californiensis* has priority (which Bergh accepted in his subsequent articles). In his other two 1879 papers, Bergh mentions the name *calensis* only in lists. Therefore, the name *Chromodoris calensis* in BERGH, 1879a and 1879b is a *nomen nudum*, and *C. calensis* Bergh, 1880, is a synonym. The valid original description of this species occurs in BERGH, 1879c, as *C. californiensis*.

The synonymy of *Hypselodoris californiensis* with *Chromodoris universitatis* and GUERNSEY's (1912) *Chro-*

modoris sp. has been long established (COCKERELL & ELIOT, 1905, and O'DONOGHUE, 1926). The new synonymization with *C. glauca* needs an explanation.

BERGH (1879b) described 2 specimens in the Berlin Museum as *Chromodoris glauca*. His text is nothing more than an external description of preserved *Hypselodoris californiensis*. The background color, arrangement of spots, and light mantle margin band are all diagnostic of *H. californiensis*. The name *C. glauca* has priority over *H. californiensis*, but *C. glauca* has appeared in the literature only once in the last 70 years (in the list of PRUVOT-FOL, 1951a: 106; she writes, "Mieux connue, cette espèce devra probablement être assimilée à l'une des *Glossodoris* bleues de California"). In contrast, *H. californiensis* is a very well-known species, reported often in the literature. To maintain stability, I treat *C. glauca* as a *nomen oblitum*, mentioning it as a synonym of *H. californiensis* only for the sake of completeness. The International Commission of Zoological Nomenclature will be petitioned to place *C. glauca* on the Official Index of Rejected Names.

Material Examined and Distribution:

California:

- 1) 1 specimen, subtidal, Santa Cruz Island; leg. R. Ames, 22 February 1963 (HB 446; CAS)
- 2) 1 specimen, 7.5 m subtidal, Anacapa Island; leg. M. Roach, 19 July 1971 (HB 410; LACM)
- 3) 1 specimen, Fisherman's Cove, Santa Catalina Island; leg. C. Swift, 14 August 1970 (HB 406; LACM A 9325)
- 4) 1 specimen, 13.5 m subtidal, Catalina Island; leg. A. J. Ferreira, October 1972 (HB 366)
- 5) 1 specimen, 15 m subtidal, Isthmus, Catalina Island; leg. A. J. Ferreira, 9 July 1975 (HB 360)
- 6) 1 specimen, 27-33 m subtidal, 2.7 km NW of Pyramid Head, San Clemente Island; leg. C. Swift, 1 July 1971 (HB 407; LACM)
- 7) 1 specimen, 13.5 m subtidal, San Clemente Island; leg. C. Gage, 18 September 1971 (HB 412; LACM A 9942)
- 8) 1 specimen, 15-18 m subtidal, Cortez Bank, Los Angeles County; leg. C. Swift, 22 September 1971 (HB 408; LACM)
- 9) 1 specimen, Newport Bay; leg. G. E. MacGinitie, 19 June 1949 (HB 441; CAS)

Explanation of Figures 63 to 68

Scanning electron micrographs of the radular teeth of *Hypselodoris californiensis* and *Hypselodoris ghiselini*

- Figure 63: *Hypselodoris californiensis*; developing lateral teeth (HB 252 B) × 675
- Figure 64: *Hypselodoris californiensis*; developing lateral teeth (HB 252 B) × 675

- Figure 65: *Hypselodoris ghiselini*; overall view of anterior portion of radula × 125
- Figure 66: *Hypselodoris ghiselini*; outermost lateral teeth × 375
- Figure 67: *Hypselodoris ghiselini*; outermost lateral teeth × 1300
- Figure 68: *Hypselodoris ghiselini*; jaw elements × 3850



Figure 63

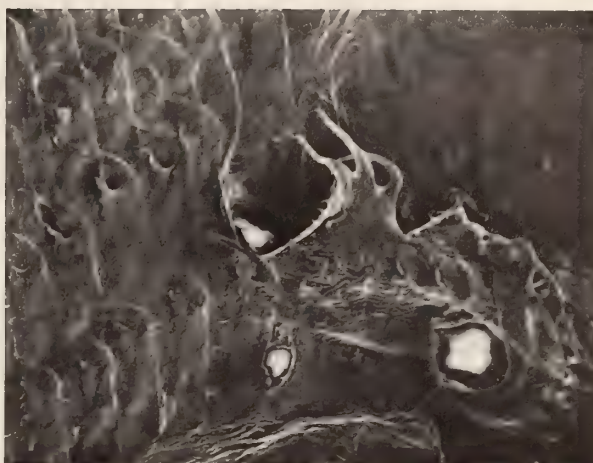


Figure 64

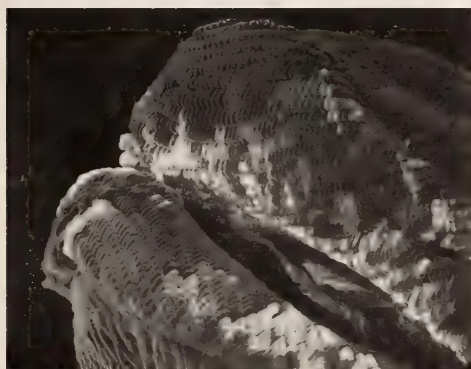


Figure 65



Figure 66



Figure 67

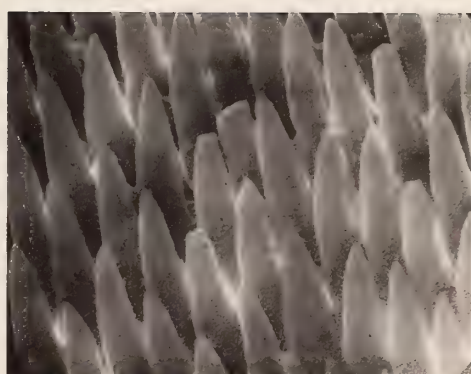


Figure 68

- 10) 1 specimen, Laguna Beach; leg. W. A. Hilton, 1915 (HB 445; CAS)
- 11) 1 specimen, Laguna Beach; leg. A. B. Burch, 15 May 1936 (HB 447; CAS)
- 12) 2 specimens, Arch Rock, Corona del Mar; leg. G. E. MacGinitie, 31 October and 29 November 1932 (HB 442 A-B; CAS)
- 13) 1 specimen, Corona del Mar; leg. G. E. MacGinitie, 26 December 1932 (HB 444; CAS)
- 14) 1 specimen, La Jolla; leg. T. D. A. Cockerell, 21 March 1902 (HB 437; CAS)
- 15) 1 specimen, San Diego; leg. A. J. Ferreira, 21 July 1974 (HB 369)

Mexico:

- 16) 4 specimens, Isla Coronado; leg. A. J. Ferreira, 28 September 1973 (HB 423 A-D; LACM A 9549)
- 17) 6 specimens, Isla San Martin; leg. A. J. Ferreira, 25 September 1973 (HB 252 and 425 A-C; LACM A9549)
- 18) 1 specimen, 6-12 m subtidal, Sacramento Reef, S of Isla San Geronimo; leg. J. McLean, 26-27 September 1971 (HB 411; LACM 71-19)
- 19) 1 specimen, 13.5-18 m subtidal, Thurloe Head (27°37' 31"N; 114°50'37"W); leg. J. McLean & P. La Follette, 23 October 1971 (HB 413; LACM 71-170)
- 20) 2 specimens, Man-of-War Cove, Bahía Magdalena; leg. J. McLean & P. La Follette, 31 October 1971 (HB 414 B-C; LACM 71-183)
- 21) 1 specimen, 23 m subtidal, on reef between Islas Calaveras Smith, Bahía de Los Angeles; leg. N. Michel & D. Mulliner, 11 October 1975 (HB 424)
- 22) 2 specimens, no data (HB 409 A-B; LACM)

It is difficult to determine the known distribution of *Hypselodoris californiensis*, because records of 3 species (*H. californiensis*, *H. agassizii*, and *H. ghiselini*) have often been lumped together. It is necessary to distinguish definite, indefinite, and incorrect records. *Hypselodoris californiensis* has been reported correctly from the following localities along the Pacific coast of California and Baja California: Monterey, Carmel, Santa Barbara County, San Pedro, Santa Catalina Island (type locality), Laguna, Newport Bay, Corona del Mar, La Jolla, San Diego Bay (see MacFarland, 1966: 162, and Sphon & Lance, 1968), and Isla Coronado (Lance, 1961). In the Gulf of California it has been reported reliably from Isla Angel de la Guarda (Farmer, 1963), and Cabo Tepoca (Puerto de Lobos), Sonora (Farmer, 1971). The Gulf of California records in Farmer (1967) and Lance (1966) are indefinite. They cannot be assigned definitely to any one of the 3 possible species. Lance's (1966: 72) statement, that Bergh (1894: 181) had reported *H. californiensis* from the region of Bahía Magdalena, is incorrect. Bergh's locality (24°11'N; 109°55'W) is in the Gulf of California between Isla Cerralvo and Las Cruces; moreover, Bergh's specimen was not *H. cali-*

forniensis, but *H. ghiselini*. MacFarland (1966: 162) lists 3 localities in the Gulf of California as collecting sites of *H. californiensis*. The first locality ("off La Paz") refers to *H. ghiselini*; the 2 collections at Puerto Peñasco are indeterminable to species. The range given in Keen (1971: 823) includes all 3 species.

The reliable occurrences of *Hypselodoris californiensis* in the Gulf of California are from Bahía de Los Angeles and Cabo Tepoca. It should be noted that the waters of Bahía de Los Angeles (to 30 m) have cooler temperatures year-round than other regions in the Gulf of California (Robinson, 1973), and a large number of Californian species have been reported in this region (data from Keen, 1971, pers. observ., and G. G. Sphon, pers. comm.). Californian species normally exhibiting tropical submergence in the Panamic province may be found intertidally and in the shallow subtidal regions of Bahía de Los Angeles.

External Morphology and Coloration:

Hypselodoris californiensis attains a length of 71 mm. The overall body color is a deep blue; large yellow dots or streaks occur on the notum (a transverse row of them anterior to the rhinophores, another row between the rhinophores, and 2 lengthwise rows along the side of the notum between the midline and the lateral edges) and in 1-2 rows along each side of the foot. The edge of the mantle and foot is bordered by a very light blue or whitish band of color (Bertsch, 1973: 109). MacFarland (1966: plt. 24, figs. 1-3) and Keen (1971: plt. 20, fig. 1) present colored illustrations of *H. californiensis*.

Radula:

The meristic characters of 32 radulae are in Table 14. The overall range of variation is 42-92 rows, with maxima of 63-150 teeth per half-row.

There is a positive correlation between the number of tooth rows and the maximum number of teeth per half-row. The regression line is described by the formula $Y = 9.48 + 1.423 X$; $r = 0.7757$, $P < 0.001$, $n = 32$.

The number of tooth rows is dependent on the radular length. The regression line formula is $Y = 36.18 + 9.28 X$. The coefficient of correlation is 0.8783, $P < 0.001$, $n = 29$.

The radular width and maximum number of teeth per half-row are positively correlated. The formula, $Y = 42.52 + 25.395 X$, describes the regression line ($r = 0.9407$, $P < 0.001$, $n = 29$).

Bergh (1879), O'Donoghue (1927) and MacFarland (1966) have described the radular teeth morphology. Figure 27 A is an outline sketch of an entire, flat-

Table 14

Radular Variation in *Hypselodoris californiensis*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
3	—	—	—	82	98
4	—	—	—	73	114
5	—	—	—	92	132
252 C	4.63	3.15	1:1.47	77	129
360	3.11	2.08	1:1.495	69	90
366	3.03	2.5	1:1.21	64	114
369	3.41	2.83	1:1.20	69	100
406	2.08	1.54	1:1.35	55	82
407	4.08	3.21	1:1.27	87	113
408	4.95	3.11	1:1.59	73	123
409 A	4.67	3.43	1:1.36	79	130
409 B	3.6	2.67	1:1.35	67	114
410	4.16	2.91	1:1.43	71	116
411	4.97	3.8	1:1.31	85	132
412	2.89	2.3	1:1.26	55	118
413	3.94	2.87	1:1.37	79	130
414 B	2.24	1.72	1:1.3	53	86
414 C	2.83	1.88	1:1.51	66	91
423 A	4.73	3.39	1:1.395	77	133
423 B	4.65	3.45	1:1.35	86	131
423 C	5.09	3.92	1:1.298	86	138
423 D	5.01	3.21	1:1.56	72	132
424	2.08	1.54	1:1.35	60	76
425 A	5.31	3.88	1:1.37	88	131
425 B	5.27	3.8	1:1.39	87	142
437	3.54	2.32	1:1.53	69	94
441	5.09	3.8	1:1.34	82	131
442 A	2.85	1.88	1:1.52	57	86
442 B	1.84	1.15	1:1.6	46	63
444	5.39	4.02	1:1.34	81	150
445	4.34	2.69	1:1.61	82	117
446	3.13	2.1	1:1.49	75	102
\bar{X}	3.89	2.8	1:1.4	73.25	113.68
s	1.108	0.824	0.116	11.769	21.58

³BERGH, 1879 C; ⁴MACFARLAND, 1966; ⁵O'DONOGHUE, 1927.

tened radula. The first lateral tooth (Figure 27 B, E-F) has a small denticle (almost forming a 3rd cusp) on the inner surface adjacent to the base of the cusps (figured also by MACFARLAND, 1966: plt. 34, fig. 12-13). The lateral teeth (Figure 27 C-D, 61) have the typical *Hypselodoris* bicuspid appearance, with denticles on the posterior surface. The extreme outermost lateral teeth become smaller, with greatly reduced cusps (Figure 62). Developing lateral teeth are shown in Figures 27 E - I, 63, and 64).

Discussion:

Hypselodoris californiensis has been mentioned frequently in the literature, but the majority of the citations are comparisons or parts of complete taxonomic listings. The species is encountered most often subtidally in southern Californian waters.

McBETH (1971b: 158) reports that *Hypselodoris californiensis* feeds on the sponge *Stelletta estrella* de Laubenfels, 1930, and *Haliclona* sp.

Hypselodoris ghiselini Bertsch, spec. nov.

(Figures 3-N, 28, 29 - 31, 65 - 68)

References and Synonymy:

- Hypselodoris californiensis* (not BERGH, 1879). BERGH, 1894: 181 - 182; pl. 7, figs. 23 - 38. MARCUS & MARCUS, 1967: 59, 176 - 178 (in part; material of locality 1); figs. 30, 32 - 33. KEEN, 1971: 823 (in part). MARCUS, 1971: 357 (in part). SPHON, 1971: 214 (in part). SPHON, 1972b: 65 (in part). MARCUS & HUGHES, 1974: 520
- Chromodoris californiensis* (not BERGH, 1879). MACFARLAND, 1966: 162 (in part; reference to Bergh's specimen from "off La Paz")
- Glossodoris californiensis* (not BERGH, 1879). ABBOTT, 1974: 355 (in part)
- Hypselodoris* sp. FARMER, 1971: 19. BERTSCH, 1973: 108 to 109. KEEN & COAN, 1975: 44. BERTSCH, 1976b: 158

Some specimens of this new species have been reported previously as *Hypselodoris californiensis*. The synonymy encompasses only those reports of specimens definitely referable to *H. ghiselini*.

The radular meristic characters of BERGH's (1894) specimen match those of *Hypselodoris ghiselini*, not those of *H. californiensis*; hence his report is actually of *H. ghiselini*.

Material Examined and Distribution:

Baja California, Gulf Coast:

- 1) **Holotype.** 2 - 3 m subtidal, Bahía Las Cruces (24°13' N; 110°05' W); leg. Michael T. Ghiselin, H. Bertsch, & J. Allen, 1 July 1974 (HB 88). This dissected specimen and its mounted radula have been deposited in the collections of the Los Angeles County Natural History Museum, LACM Type Series, No. 1849
- 2) **Paratypes.** 2 specimens, 2 - 3 m subtidal, Nopolo and Juncalito; leg. H. Bertsch, M. Ghiselin, and J. Allen, 27 June 1974 (HB 86 A-B)
- 3) 1 specimen, intertidal, Puertecitos; leg. H. Bertsch, T. M. Gosliner, and G. C. Williams, 27 March 1972
- 4) 2 specimens, subtidal, Isla San Marcos; leg. E. Janss, Jr., April 1974 (HB 432 A-B; LACM A 9555)
- 5) 1 specimen near Loreto; leg. M. Ghiselin, H. Bertsch, and J. Allen, 27 June 1974 (HB 87)
- 6) 1 specimen, Notri; leg. H. Bertsch, M. Ghiselin, and J. Allen, 4 July 1974 (HB 89)
- 7) 4 specimens, 14 m subtidal, S end of Isla San Diego; leg. E. Janss, Jr., April 1974 (LACM)
- 8) 1 specimen, Los Islotes; leg. A. J. Ferreira, July 1971 (identified from a color transparency)
- 9) 1 specimen, intertidal, San Gabriel Bay, Isla Espíritu Santo (24°29' N; 110°27' W); leg. G. G. Sphon, 31 March 1974 (HB 431; LACM 74-31)
- 10) 1 specimen, Las Cruces; leg. G. Lombard, July-August 1972 (HB 100 A)

- 11) 1 specimen, 3 - 4 m subtidal, bay N of Punta Gorda, 8 km S of Las Cruces; leg. H. Bertsch, 22 July 1972 (HB 26)

Mainland Mexico, Gulf Coast:

- 12) 6 specimens, Puerto Peñasco, Sonora; leg. P. Pickens, 9 June 1964 and 15 June 1965 (HB 318 A-F; USNM 753560; this is the material from locality 1 of MARCUS & MARCUS, 1967: 176 - 178)
- 13) 2 specimens, Cabo Tepoca, Punta Lobos, Sonora; leg. F. & R. Poorman, October 1975 (HB 428 A-B; LACM A 8477)
- 14) 3 specimens, intertidal, Bahía San Carlos, Sonora; leg. F. & R. Poorman, October 1975 (HB 427 A-C; LACM A 8477)
- 15) 3 specimens, intertidal, Bahía San Carlos; leg. F. & R. Poorman, 1 December 1975 (HB 429, 430 A-B; LACM A 8477)
- 16) 1 specimen, Guaymas, Sonora; leg. A. Kerstitch, July 1971 (identified from a color transparency)

The type locality of *Hypselodoris ghiselini* is Las Cruces, Baja California del Sur, Mexico. It has been collected from numerous intertidal and subtidal localities throughout the Gulf of California. The known range is nearly the entire Baja California Gulf coastline, from Puertocitos to Punta Gorda, and on the mainland Mexico coast from Puerto Peñasco to Guaymas.

External Morphology and Coloration:

Holotype specimen measured 35 mm total length when alive. Lengths of other living animals were 30, 57, 66, and 69 mm.

Coloration of animal a deep navy blue (color illustration in MARTIN, 1977: 18); the notum is covered with numerous small, bright yellow specks. Along the side of the body are 4 - 5 irregular rows of many small bright yellow maculations. There are whitish-blue spots scattered on the notum; they are far less numerous than the yellow markings, and vary in number from just a few to over a dozen. Bottom of the foot is unmarked, a solid deep blue color. Rhinophores and gills are navy blue, with yellow dots on the inner sides of the gills. Seven specimens had 9 - 12 gills each; one specimen had 17 perfoliations to each rhinophore.

Radula:

The sizes, counts, and means of meristic characters of 23 radulae are presented in Table 15. The combined radular formula is 43 - 83 (50 - 128 · 0 · 50 - 128).

The number of tooth rows and maximum number of teeth per half-row are positively correlated (Figure 29). The regression line formula is $Y = -18.34 + 1.7 X$ ($r = 0.8895$, $P < 0.001$, $n = 23$).

Table 15

Radular Variation in *Hypselodoris ghiselini*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
6	—	—	—	70	93
26	4.36	3.31	1:1.32	77	128
86 A	4.24	3.05	1:1.39	75	113
86 B	4.4	3.43	1:1.28	81	126
87	4.46	3.54	1:1.26	78	123
88	1.88	1.25	1:1.15	51	72
89	3.86	3.07	1:1.26	79	123
100 A	2.63	1.62	1:1.62	62	89
318 A	4.65	2.66	1:1.75	83	113
318 B	3.13	1.82	1:1.72	69	89
318 C	3.19	1.74	1:1.83	71	79
318 D	2.32	1.52	1:1.53	58	76
318 E	4.08	2.12	1:1.92	74	102
427 A	3.31	2.2	1:1.5	60	87
427 B	2.48	1.45	1:1.71	55	82
427 C	1.25	0.77	1:1.62	43	50
428 A	2.61	1.8	1:1.45	56	75
428 B	3.35	2.46	1:1.36	66	96
429	1.82	1.05	1:1.73	53	55
430 A	3.37	2.18	1:1.55	54	86
430 B	2.12	1.55	1:1.37	49	67
431	3.21	2.55	1:1.26	57	98
432 B	2.99	1.98	1:1.51	60	79
\bar{X}	3.169	2.14	1:1.5	64.39	91.35
s	0.96	0.786	0.213	11.47	21.97

⁶MARCUS & MARCUS, 1967.

Regression analysis (Figure 30) shows also that the number of rows is dependent on the length of the radula ($Y = 28.84 + 11.138 X$). The coefficient of correlation is 0.9181, $P < 0.001$, $n = 22$.

The radular width and maximum number of teeth per half-row are positively correlated (Figure 31). The formula, $Y = 32.8 + 27.296 X$, describes the regression line ($r = 0.9545$, $P < 0.001$, $n = 22$).

Tooth morphology has been described by MARCUS & MARCUS (1967) and BERGH (1894). Figure 65 is an *in situ* view of the anterior portion of the radula. The innermost lateral tooth in each half-row (Figure 28 A-E) has a lengthwise flange along the inner side of the base; there is a single denticle (long enough to give a tricuspid appearance to the distal portion of the tooth shaft) on the inner face at the level of the cusp bases. The outer

face has 3 - 4 denticles. Towards the middle of the tooth row the teeth increase in length, with 4 - 10 denticles ($\bar{X} = 7.23$, $s = 1.46$, $n = 42$) on the posterior surface (Figure 28 F-H). The outer lateral teeth (Figures 66, 67) decrease in size, with the cusps becoming shorter and the base of the shaft thickening along the antero-posterior axis.

Figure 28-I and R - U show developing teeth in progressively more anterior rows. A sequence of developing teeth from the most posterior row is shown in Figure 28 J - Q. Older teeth are towards the more lateral portions of the tooth row. Tooth growth proceeds from the outer margins towards the center of the half-row, and as the tooth rows become progressively more anterior.

Jaw elements (Figures 28 V - Y and 68) are triangular, with pointed ends.

Discussion:

The external coloration of *Hypselodoris ghiselini* readily distinguishes it from *H. californiensis*. The yellow maculations are much smaller (always dot-like) and more numerous in *H. ghiselini*; there is no light color band on the edge of the notum and the background color is darker. *Hypselodoris californiensis* has larger (and fewer) yellow marks, that often are in the form of elongate streaks, and a light-colored band surrounding the edge of the mantle margin. These are not ontogenetic characters, because these differences exist for large and small specimens of both species.

Etymology:

This species is named after Dr. Michael T. Ghiselin, who collected the holotype specimen, in recognition of his work on opisthobranch phylogeny.

Hypselodoris lapolislazuli (Bertsch & Ferreira, 1974)

comb. nov.

(Figure 30)

References and Synonymy:

- Thorunna lapolislazuli* BERTSCH & FERREIRA, 1974: 343-345; figs. 1, 5-9. KEEN & COAN, 1975: 44. BERTSCH, 1976b: 158.

Material Examined and Distribution:

No additional specimens have been found since the type lot. *Hypselodoris lapolislazuli* is known only from the Galápagos Islands.

External Morphology and Coloration:

Preserved lengths of the 4 known specimens vary from 4-6 mm. Coloration consists of light blue, navy blue, and orange yellow (BERTSCH & FERREIRA, 1974: fig. 1). An irregular dorso-median stripe of light blue begins anterior to the rhinophores, widens just behind the rhinophores and then becomes thinner, continuing back to just before the gills. A large area of dark navy blue completely encloses the mid-dorsal light blue stripe, with a patch of navy blue extending across the notum at about $\frac{1}{2}$ the animal's length. This navy blue region is randomly covered with dots and splotches of orange and light blue. The mantle is edged completely by a light blue band. The tail protrudes out behind the posterior portion of the mantle, and has a navy blue streak down its center, which is dotted with orange patches; a light blue band occurs on the border of the foot. The 6 simply pinnate gills and the rhinophores are navy blue, with whitish tips.

Radula:

The known radular formula is $41 (47-51 \cdot 0 \cdot 47-51)$. The teeth are typically bicuspid (see the scanning electron micrographs in BERTSCH & FERREIRA, 1974: figs. 5-9), with up to 5 denticles on the posterior surface below the secondary cusp of the erect shaft.

Discussion:

Reexamination of scanning electron micrographs of the radula, and a better understanding of the genus *Thorunna* necessitate the shift of this species to *Hypselodoris*. What was thought to be a thin prong on the inner face of the innermost lateral tooth is actually the dorsal portion of an upward-curved flange that runs lengthwise along the inner side of the tooth. Such a flange occurs in other species of *Hypselodoris* (e.g., *Hypselodoris ghiselini*, fig. 28 A, and *H. ruthae* Marcus & Hughes, 1974, pers. obser.). The width and shape of the innermost tooth of *H. lapolislazuli* is not the extremely broad-based shape (becoming at least twice as wide posteriorly as it is anteriorly) of *Thorunna*, and should not be included in that genus. The genus *Thorunna*, therefore, is not known from the Pacific coast of America, but is confined to the Indo-Pacific basin, north to Japan and east to Hawaii.

Hypselodoris lapolislazuli has a color pattern similar to *Mexichromis tura* and *M. antonii*, but each has distinctively different patterns. *Hypselodoris lapolislazuli* has a light blue margin, yellow-orange dots on a deep blue background on the mid-lateral portions of the notum, with a light blue patch down the center of the notum. *Mexichromis antonii* has yellow and black bands surrounding the free edge of the notum, with a light blue background color on which are streaks and patches of darker blue laterally, and magenta and white centrally. *Mexichromis tura* has a yellow band around the free edge of the notum, followed by a light blue region surrounding the lateral portions of the notum, with a dark blue central region in which are numerous small yellow dots.

Discussion of *Hypselodoris*

Too few specimens of *Hypselodoris lapolislazuli* are known to compare it statistically with the other 3 species of *Hypselodoris* from the Pacific coast of America; the other 3 can be reliably distinguished from radular characteristics, in addition to the coloration differences already noted. Significant differences between these species are summarized in Table 16. The means used to calculate the t-tests are given in Tables 13-15. *Hypselodoris californiensis* has a larger and wider radula, with more tooth rows and

Table 16

Results of t-tests Conducted between Species Pairs
of 3 American Pacific Coast *Hypselodoris*.

Numbers are significance probabilities (P). N.S.: not
significant, no difference between the species for the
particular measurement or count.

<i>Hypselodoris:</i>	<i>californiensis</i>	<i>ghisellini</i>
<i>agassizii</i>		
Rows/teeth	N.S.	N.S.
Length/rows	N.S.	N.S.
Width/teeth	N.S.	N.S.
Length	<.01	N.S.
Width	<.01	N.S.
W:L ratio	N.S.	N.S.
Rows	<.01	N.S.
Max. teeth	<.001	N.S.
<i>californiensis</i>		
Rows/teeth		N.S.
Length/rows		N.S.
Width/teeth		N.S.
Length		<.02
Width		<.01
W:L ratio		<.05
Rows		<.01
Max. teeth		<.001

a larger maximum number of teeth per half-row than *H. agassizii*, but the width:length ratios of these 2 species are the same. The denticles on the inner lateral teeth also distinguish *H. californiensis* from *H. agassizii*. *Hypselodoris californiensis* is larger in all measured parameters (including the width:length radular ratio) than *H. ghisellini*. It is important to emphasize that the width:length ratio is different, because this excludes the possibility of the radular differences being ontogenetic. The coloration differences have been discussed already. *Hypselodoris agassizii* and *H. ghisellini* are identical in their meristic characters. However, the presence or absence of denticles on the inner lateral teeth clearly separates the 2 species.

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ERRATUM

Mr. Gary McDonald recently informed me that the International Commission on Zoological Nomenclature had ruled on the spelling of *Chromodoris mcfarlandi* Cockerell, 1901. At the request of D. P. COSTELLO (1947), the Commission (1950: 430-431) officially emended the spelling of the species name to *C. mcfarlandi*. Accordingly, my comments (BERTSCH, 1978: 314) on the re-establishment of the original spelling are superfluous and erroneous.

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The Effects of an Ectoparasitic Gastropod,
Caledoniella montrouzieri,
upon Molting and Reproduction of a Stomatopod Crustacean,
Gonodactylus viridis

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(2 Text figures)

INTRODUCTION

SEVERAL AUTHORS have reported the occurrence of a snail living upon mantis shrimps, and the morphology and familial affiliation of this unique gastropod, *Caledoniella montrouzieri*, Souverbie, 1869, have been most completely discussed by ROSEWATER (1969). The host stomatopod usually carries two snails, a smaller male on the posterior ventral thorax, and a larger female at the base of or on the anterior surface of the fifth pleopod. The female snail apparently moves on the ventral abdomen of the stomatopod, since egg capsules are attached to the surfaces of the host pleopods. Although THIELE (1929) described a radula, ROSEWATER (op. cit.) found only a muscular proboscis with no radula in three dissections, leaving the nutritional mode of these snails in doubt. However, ROSEWATER (op. cit.) observed that the tips of the thin pleopodal gills of the stomatopods appeared damaged, and suggested that the gastropods may suck body fluids from the host stomatopod. Rosewater found no other evidence of penetration of the host exoskeleton, but mentioned a mucoid deposit at the site of the snail's attachment to the host. These snails occur on several species of gonodactylid stomatopods in different localities, including *Gonodactylus chiragra*, *G. smithii*, *G. platysoma*, *G. falcatus*, *G. mutatus*, *G. viridis*, and *Gonodactylolus paulus* in Madagascar, the Comores Islands, Réunion, the Persian Gulf, the Andaman Islands, Thailand, Indonesia, Australia, New Caledonia, and Samoa (ROSEWATER, 1969, 1975; MANNING, 1968, 1969, and personal communication; personal observations).

This paper investigates the effects of *Caledoniella montrouzieri* upon molting rate, growth, and reproduction of *Gonodactylus viridis*. Although *G. viridis* co-occurs with six

other species of Gonodactylidae (*G. chiragra*, *G. smithii*, *G. falcatus*, *G. ternatensis*, *Haptosquilla glyptocercus*, *Pseudosquilla ciliata*) on a large tide flat at Phuket, Thailand, where the study was conducted, the snail occurred exclusively on *G. viridis*. The term "parasite" will be used in the broad sense of an organism which imposes a negative effect upon its host, without specification of the mechanisms of inflicting the negative effect.

METHODS

The stomatopods were collected from their coral rubble habitat, measured, their parasitic condition (including ovipositions by the snails) noted, and maintained individually in plastic bowls and aquaria with normal laboratory lighting at the Phuket Marine Biological Center. Field and laboratory temperatures approximated 26°-27° C. The stomatopods were fed crustaceans and mollusks and the water was changed every second or third day. The stomatopods were examined daily for molts and ovipositions. Stomatopods can be successfully maintained, showing normal growth and reproduction, for as long as a year using these methods; the stomatopods were maintained at Phuket about six weeks (see REAKA, 1975, 1976). At the end of the study the stomatopods were killed and preserved in 10% formalin, then changed to 70% ethyl alcohol. The snails remained attached throughout this treatment.

Molting frequencies are too low in stomatopods to establish molting rates for individuals. The most reliable measure of molting frequency in stomatopods is the population molting rate, MR, derived from the total molts in the sample population/total number of stomatopod maintenance

days ($MR = \Sigma M / \Sigma SMD$). This index of molting rate provides results consistent with a variety of other field and laboratory methods used independently to assess the frequency of molting in populations, and is least influenced by sample sizes, maintenance time, and the effects of slowly or rapidly molting individuals in the populations. Molting rate does not decline with increased maintenance time (REAKA, 1975). The several species of stomatopods at Phuket, including the parasitized and nonparasitized *Gonodactylus viridis*, were maintained simultaneously for relatively short periods of time under identical conditions. To assess the reliability of the MR, population molting rates were calculated for each of 10, 6, 5, and 4 independently collected subpopulations of four other species (*Gonodactylus zaca*, *G. falcatus*, *G. chiragra*, and *Pseudosquilla ciliata*). The sample sizes of these subpopulations approximated those of the parasitized and nonparasitized *G. viridis*. The standard errors (SE) of the MR, calculated from the molting rates of each of these subpopulations were 0.039, 0.030, 0.012, and 0.022 for the 4 species respectively. The subpopulations of *G. zaca*, *G. falcatus*, and *P. ciliata* were maintained over different seasons and years, although the five subpopulations of *G. chiragra* were maintained simultaneously at Phuket. These results indicate that the MR values presented for the parasitized and nonparasitized *G. viridis*, as well as the other species from Phuket which were maintained simultaneously with *G. chiragra*, probably are reliable within approximately 0.01 or at most 0.04 MR units (see REAKA, 1975, 1978).

Molting growth increments (G/M) were determined by measuring nine linear characters of the exuvium and the hardened postmolt exoskeleton (see REAKA, 1975, 1978), which represented most of the major body dimensions. Growth was determined by the percentage difference between the postmolt and premolt exoskeletons and averaged for all of the nine morphological characters.

Reproductive condition was assessed by the presence of extruded egg batches carried by the females.

RESULTS

Of the 56 parasitized *Gonodactylus viridis*, four were occupied by a single rather than two *Caledoniella montrouzieri*. The anterior (male) snail was missing in two cases, the posterior (female) snail was lost in one, and the site of loss was undetermined for one individual. These results suggest that there was no differential loss or failure to colonize the anterior or the posterior attachment site on the host stomatopod.

One stomatopod carrying a pair of reproductive snails molted overnight; the snails and their eggs subsequently

were found intact on the postmolt host. Unfortunately I was unable to observe the behavioral events which allowed the snails either to remain in place or regain their position while the exuvium was shed. Also, the fate of the eggs deposited prior to the molt was not determined. Presumably they were eaten along with the exuvium by the stomatopod, and the snail deposited new egg cases upon the postmolt stomatopod.

Caledoniella montrouzieri occurred on 13.4% of the population of *Gonodactylus viridis*. The snails occurred and reproduced on both sexes of stomatopods over a wide range of sizes. *G. viridis* acquire adult sexual morphology at 15 mm in length, although they continue to molt and grow throughout their life. Snails parasitized only stomatopods ≥ 15 mm in length. Considering all individuals beyond this size, Figure 1 shows that parasitized *G. viridis* were smaller than nonparasitized individuals ($\bar{X} = 29.5, 34.2$ mm; $p < 0.001, t = 3.9; N = 56, 345$). If juvenile stomatopods (< 15 mm) were also included, the t -test value ($\bar{X} = 29.5, 34.1; t = 1.9; N = 56, 361$) fell just below the critical statistic for $p < 0.05$ that parasitized individuals were smaller than nonparasitized stomatopods. Two observations, however, suggested that the juvenile stomatopods did not represent available hosts and should not be included in the samples comparing body size in parasitized

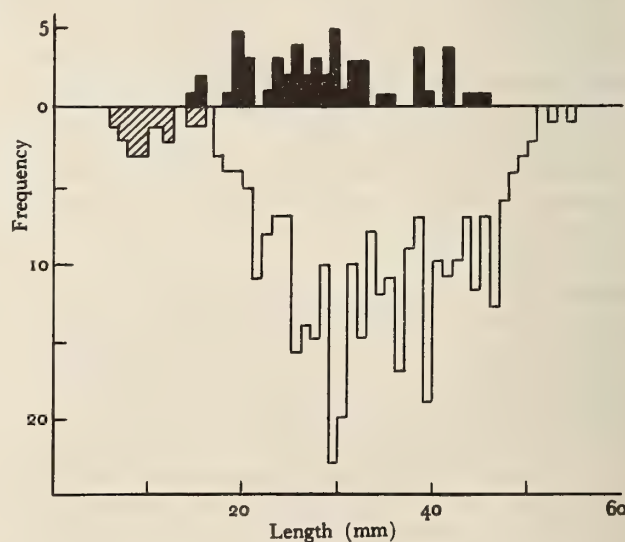


Figure 1

Frequency distribution and body size (total length) of *Gonodactylus viridis* which are not parasitized (open histogram) and parasitized (black histogram) by *Caledoniella montrouzieri*. Hatched histogram indicates juvenile *Gonodactylus viridis*

vs. nonparasitized *G. viridis*. Although 14.0% (56/401) of mature *G. viridis* were parasitized, none of the 16 juveniles collected were parasitized (0/16 rather than the expected 2.24/16). In addition, although adult snails showed extreme site specificity on the host, small snails showed some irregularity in their site of attachment, suggesting that they initially colonize small but sexually mature stomatopods. Therefore, considering samples of sexually mature hosts, the presence of snails definitely is associated with small size of the host.

These results suggest either that the snails inhibit growth of the host, or that the snails prefer small hosts or are selectively removed from large hosts. The four stomatopods occupied by single rather than both snails ranged from 16-55 mm in body length, and showed no trend for large hosts of either sex to remove or lose parasites more efficiently than small hosts. Therefore, the effects of the snails upon the molting rate of the hosts were examined.

Of 361 nonparasitized individuals, 4.2% molted during the relatively short period of maintenance (10/182 females, 4/163 males, and 1/16) juveniles; of 56 parasitized individuals (35 females, 21 males), only one female (1.8%) molted. The number of stomatopod maintenance days/molt for the nonparasitized population sample was 571 days, while the number of days/molt for the parasitized sample was 1415 days. The molting rates (MR) calculated for the nonparasitized and parasitized subpopulations were 0.18 and 0.07, respectively ($SE \approx 0.01$, see above). Figure 2 shows the molting rates calculated for the seven sympatric species of gonodactylids from Phuket. Compared to the

MR for other species, which increase regularly with body size in this and other stomatopod assemblages (REAKA, 1975, 1978), and to the MR for nonparasitized *Gonodactylus viridis*, parasitized individuals showed significantly depressed molting rates.

Growth increments were available for only three *Gonodactylus viridis* because molting individuals eat their exuvium. The %G/M for the parasitized female was 2.8%, while the two nonparasitized females grew 2.8% and 5.0%, respectively.

Of 182 nonparasitized female *Gonodactylus viridis*, 32 females (17.6%) carried egg batches; of 35 parasitized *G. viridis* females, none were ovigerous ($p=0.003$, Fisher exact probability test). These results suggest either that females which bear snails do not reproduce, or that snails do not live on or are removed from reproductive female stomatopods.

DISCUSSION

This study pertains to two questions: (1) the nutritional biology of *Caledoniella montrouzieri*, a gastropod formerly classified as commensal upon its stomatopod host; and (2) the co-evolutionary biology of a sessile organism which lives upon a crustacean host which must molt to grow.

The smaller body size of parasitized than nonparasitized stomatopods suggests that the snail in some way may inhibit growth of the host, although these results also could be obtained by avoidance of or selective removal from large host individuals. No observations suggest that snails selectively avoid large stomatopod hosts. Also, there is no evidence that large stomatopods lose snails more frequently than small hosts, since molting frequencies which might lead to shedding of parasites do not change over ontogeny in stomatopods (REAKA, 1975, 1978), and since single snails are not differentially lost by large host stomatopods. In contrast, several lines of evidence suggest that the presence of snails inhibits growth. Lower percentages of parasitized than nonparasitized individuals molt. Infected stomatopods show longer intermolt intervals and lower molting rates (MR) than noninfected hosts. No effect of the snail upon molting growth increment could be detected, but samples were too small to permit any conclusions.

Failure of parasitized stomatopods to reproduce may result from mechanical obstruction to mating, since the male snail occupies the 7th sternal ridge directly posterior to the ovopore of the stomatopod. The ventral copulatory tubes of the male stomatopod are inserted into the seminal vestibule on the 6th thoracic sternite of the female; copulation may be prerequisite for ovoposition and may be prevented by the presence of the snail. It seems unlikely that snails either avoid reproductive females or that reproductive

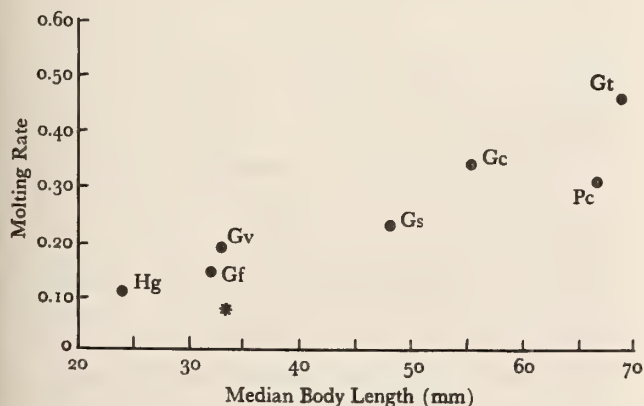


Figure 2

Relationship of molting rate (MR) to body size in 7 populations (closed circles) of nonparasitized stomatopods which were maintained simultaneously in Phuket, Thailand. The closed circle for *Gonodactylus viridis* (Gv) refers to the nonparasitized population sample, and the star refers to the parasitized population sample of *Gonodactylus viridis*. Refer to the text for explanation and reliability measures of MR and for explanation of species.

females are completely effective in removing snails. Considered in combination with the effects of the snail upon molting frequencies, it seems possible that the snails obtain nutrients from the host stomatopod and therefore inhibit reproduction. Regardless of the proximate cause, parasitism by snails imposes complete reproductive failure upon the host stomatopod.

Therefore, *Caledoniella montrouzieri* inflict both decreased growth rates and reproductive failure upon their host. These results support ROSEWATER's (1969) suggestion that the snails, even though lacking a radula, may obtain nutrients by sucking on the thin abdominal gill filaments of the host stomatopod. An alternative and not mutually exclusive hypothesis derives from the disadvantage of host molting for the gastropod, which may lead to selection for the snail to provide some misinformational cue which inhibits molting of the host. The integration of molting in Crustacea is known to be complex and mediated by neuroendocrines (HIGHNAM & HILL, 1969). Although one pair of snails successfully survived and reattached after the molt of the host, four stomatopods carried only one snail, indicating that snails occasionally lose their host; molting of the host seems a logical time for loss to occur. Also, molting of the host probably inflicts considerable loss of reproductive investment upon the snail. Therefore, there may be a selective advantage for the snail to inhibit molting in the host either by neuroendocrinological cues or by depleting the energy supply of the host. Obtaining nutrients may not only decrease the probability of the host molting, but also reaps obvious energetic benefits for the parasite. Therefore, progression from a commensal to a parasitic condition may occur very rapidly in symbioses of arthropods with indeterminate molting and growth.

In addition, molting rates may be instrumental to the extreme specificity of *Caledoniella montrouzieri* on *Gonodactylus viridis* at Phuket, where six other morphologically and behaviorally similar species of gonodactylids occur on the same tide flat. *G. viridis* is a small, abundant species with a low intrinsic molting rate which is further lowered by the presence of the snail. Large species of sympatric stomatopods molt frequently (see Figure 2) which may prevent effective parasitism by the snails. Other small species with low molting rates (*G. falcatus*, *Haptosquilla glyptocerus*) are less abundant than *G. viridis* at Phuket. Thus, successful parasitism of the snail on other species of stomatopods may not be feasible.

SUMMARY

1. Pairs of the symbiotic gastropod *Caledoniella montrouzieri* occurred on 13.4% of a population of gonodac-

tylid stomatopods, *Gonodactylus viridis*, in Phuket, Thailand. Individual snails were lost in 4/56 cases, but there was no differential loss of anterior (male) or posterior (female) snails and no differential loss according to size or sex of the host. One pair of snails survived and reattached after their host molted.

2. Sexually mature stomatopods which carried pairs of the gastropod were smaller than sexually mature individuals not carrying snails. Juvenile stomatopods did not bear snails.

3. Lower percentages of stomatopods which carried snails molted than those which did not carry snails, although samples were too small for statistical significance. Molting intervals were longer and molting rates were lower for parasitized than nonparasitized *Gonodactylus viridis*; molting rates for parasitized individuals also were low compared to size-specific molting rates for other sympatric species of gonodactylid stomatopods. The snails inflicted no detectable effect upon growth per molt in the three cases observed.

4. Oviposition of *G. viridis* was completely inhibited by the presence of snails.

ACKNOWLEDGMENTS

I wish especially to thank Edward Bird, Joseph Rosewater, Raymond Manning, Alan Kohn, Roy Caldwell, and Ralph Smith for their interest and valuable comments. This work was supported by NSF Grant GB-37046.

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Notes on the Cephalopods of Monterey Bay, California, with New Records for the Area

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(4 Text figures)

INTRODUCTION

ALTHOUGH THE DISTRIBUTION and abundance of cephalopods has been studied extensively along the coast of western North America, the literature on these mollusks in Monterey Bay, California, has been brief. HOYLE (1904) and BERRY (1912a) reviewed the first extensive cephalopod collections from the Pacific coast made by the U.S. Fish Commission steamer *Albatross* and BERRY (1912a) recorded 11 species taken in Monterey Bay. SMITH & GORDON (1948) listed 15 species known from the bay at the time but added no new records of their own. Cephalopods caught chiefly by commercial fishing in the area have been reported by BARTSCH (1935), CLARK & PHILLIPS (1936), CLASSIC (1929, 1949), CROKER (1937), FIELDS (1950, 1965), PHILLIPS (1933, 1934, 1941, 1961), and SCOFIELD (1924).

More recently other authors have surveyed the pelagic cephalopod fauna of certain geographic areas of the Pacific coast. MCGOWAN (1967) and OKUTANI & MCGOWAN (1969) examined the distribution of the cephalopods in the California Current system, most of which were taken off southern California. YOUNG (1972) revised the taxonomy of the eastern Pacific pelagic cephalopod fauna based on thousands of specimens primarily from off southern California. PEARCY (1965), PEARCY *et al.* (1977) and ROPER & YOUNG (1975) have analyzed the vertical distribution of pelagic cephalopods based on midwater trawl surveys. As a result of these works, the distribution of most pelagic cephalopods now known from Monterey Bay has been updated.

The ecological and taxonomic literature on eastern North Pacific benthic octopods is sparse, but some work has appeared based on specimens caught in Monterey Bay. FISHER (1923, 1925) reported on the brooding habits of a

small subtidal species (cf. *Octopus rubescens*) caught in the bay. PHILLIPS (1934) reviewed the octopod fishery in California, much of which was then concentrated in Monterey Bay, and elaborated on each nominal species. WARREN *et al.* (1974) caught tidepool-dwelling *O. rubescens* in the bay and studied color changes. BALLERING *et al.* (1972) observed evenomation in *O. rubescens* also caught intertidally in the bay.

Despite the fact that most species known from Monterey Bay were discussed in the literature above, there has been no report on the cephalopods from the bay since SMITH & GORDON (1948). This paper reports on the cephalopods collected with closing trawls by Moss Landing Marine Laboratories (MLML) and Steinhart Aquarium, San Francisco (MCCOSKER & ANDERSON, 1976), provides information on the vertical distribution of some species that occur in Monterey Bay and increases the number of species known from this area.

MATERIALS AND METHODS

Most specimens of pelagic cephalopods detailed in this study were taken from the bay during the bimonthly Steinhart Aquarium Midwater Maintenance Program (SAMMP) cruises with a modified, 1.8 m Tucker trawl (TUCKER, 1951). The 9 mm mesh net was outfitted with a messenger operated, double-release mechanism and a flow-through, canvas cod end bag (see BAKER *et al.*, 1973). The net was towed at about two knots from the R/V *ST-908*, a 16.5 m converted harbor tug on loan to MLML from Scripps Institution of Oceanography. Two to four one hour hauls per cruise resulted in 56 discrete depth samples grouped in 100 m intervals from the surface to 800 m. Additional specimens were obtained from seven ½ hour hauls in the upper 100 m. Tow depth was determined by reading

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the disc charts from a Benthos Time-Depth Recorder, model 1170. A total of 151 specimens of pelagic cephalopods was thus collected from two areas in Monterey Canyon between 27 August 1974 and 23 January 1976 (Figure 1).

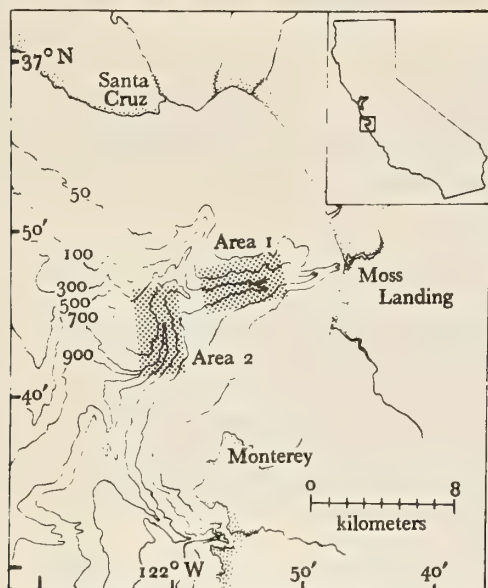


Figure 1

Map of Monterey Bay, California, showing the SAMMP trawling areas. Contours in fathoms

In addition to the above samples, two cruises of the USNS *De Steiguer* resulted in nine successful hauls with a 2.2 m beam trawl on the lower continental slope off Monterey Bay and in the canyon. Two new benthic octopods were taken by a party of MLML students.

Specimens were fixed in 10% formalin for several days, rinsed in water and stored in 70% ethanol. All specimens reported here as new to the area have been deposited in the collection of the Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, or the Museum of Moss Landing Marine Laboratories. Identifications of pelagic specimens were made utilizing the key in YOUNG (1972). In all cases the dorsal mantle length (DML) was measured as an indication of body size. All measurements are in millimeters (mm) unless otherwise indicated. The vertical distribution of the two most abundant pelagic cephalopods (young of *Gonatus onyx* and *Galiteuthis phyllura*) was calculated on a catch per unit effort basis by plot-

ting the average number taken per hour of trawling in each 100 m interval divided by the total number of tows, 63.

FAMILY ACCOUNTS

The species of cephalopods presently known from Monterey Bay are discussed below. Ten species have not been reported previously from the bay: *Gonatus onyx* (BERRY'S, 1912a, records of *G. fabricii* probably are this species, at least in part), *Gonatus californiensis*, *Gonatopsis borealis*, *Berryteuthis anonychus*, *Chroteuthis calyx*, *Octopoteuthis deletron*, *Valbyteuthis danae*, *Japetella heathi*, *Granelledone* sp. and *Benthocopus* sp. New data, chiefly regarding the recent occurrences are presented below. The relative abundances of cephalopods from the 63 closing net samples are given in Figure 2. For most species, only the

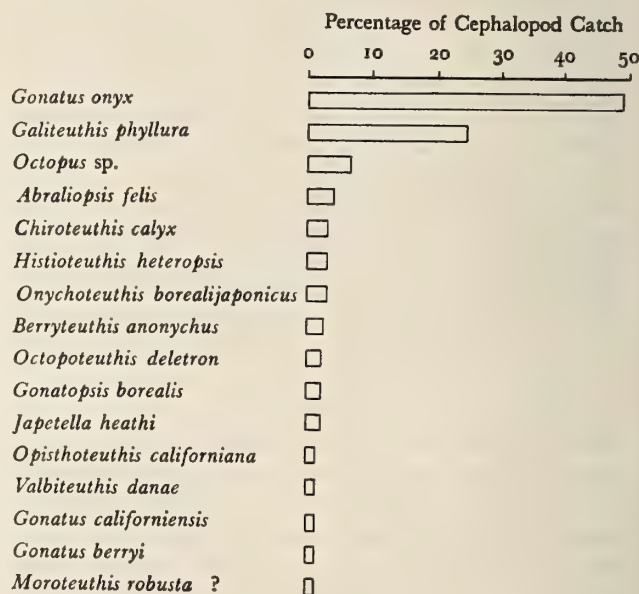


Figure 2

Percent composition of pelagic cephalopods in the SAMMP mid-water trawl catches; N = 63 samples

young are represented and exact populational abundances are not known due to probable net avoidance of larger individuals, especially during the day.

SEPIOIDEA

SEPIOLIDAE

Rossia pacifica Berry, 1911

The common benthic sepiolid, *Rossia pacifica* often is taken in bottom trawls between about 40 and 250 m in the bay. Over twenty specimens have been taken by MLML in recent years and it appears to be absent over coarse sand, preferring instead muddy bottoms.

TEUTHOIDEA

LOLIGINIDAE

Loligo opalescens Berry, 1911

Loligo opalescens is the only commercially fished cephalopod in Monterey Bay today; over 7,000 tons were landed at the bay's 3 ports in 1974 (McALLISTER, 1976). Fishing grounds stretch from south of the Salinas River to west of Monterey in depths of about 20 to 50 m. This is also the chief spawning area for the species. FIELDS (1965) detailed the general biology of *L. opalescens* and a recent symposium held at the annual California Cooperative Oceanic Fisheries Investigations (CalCOFI) meetings has updated our knowledge of this cephalopod, the results of which are to be published in the CalCOFI Reports. The reader is referred to this publication for most of the literature on *L. opalescens*.

ENOPLOTEUTHIDAE

Abraliopsis felis McGowan & Okutani, 1968

Only eight specimens of *Abraliopsis felis* (8-38 mm DML), a relatively abundant offshore squid (OKUTANI & McGOWAN, 1969), were taken during the SAMMP program inside the bay. It is one of the most frequently encountered prey species of albacore caught off central California, but its appearance in Monterey Bay probably is occasional. Because of changes in length frequencies, PEARCY (1965) suggested the species may be a seasonal breeder in near-shore waters off Oregon during the summer.

OMMASTREPHIDAE

Dosidicus gigas d'Orbigny, 1835

The jumbo squid, *Dosidicus gigas*, enters Monterey Bay infrequently (BARTSCH, 1935; CLARK & PHILLIPS, 1936;

CROKER, 1937; PHILLIPS, 1933). Clark and Phillips listed the northernmost capture locality for this species as 20 miles north of Santa Cruz, which apparently is still valid. Known to attain 1.5 m DML off Peru (see WORMUTH, 1974), Monterey Bay specimens have generally measured less than about 350 mm DML (CLARK & PHILLIPS, 1936; personal observations of five specimens taken in 1974 and 1976).

HISTIOTEUTHIDAE

Histioteuthis heteropsis (Berry, 1913)

Although infrequently encountered above 500 m in Monterey Bay, ten specimens of *Histioteuthis heteropsis* (12-128 mm DML) have been captured recently. Five mid-water trawl collections were below 400 m during the day, one in 300 m at night captured two specimens. One specimen (76 mm DML) was found dead on the beach in front of MLML after strong winds in March, 1975. Generally voracious in the aquarium, specimens have lived a maximum of four days at 7°C (McCOSKER & ANDERSON, 1976).

OCTOPOTEUTHIDAE

Octopoteuthis deletron Young, 1972

Two specimens of *Octopoteuthis deletron* (24, 102 mm DML) were taken in the closing midwater trawl at 190 and 500 m, both during the day. In addition to these, 1 specimen was identified from the stomach of the slope-dwelling fish *Antimora microlepis* captured in a beam trawl in 1390 m, suggesting the squid was swimming close to the sea floor. The fish is not known to swim far off the bottom in search of prey.

GONATIDAE

Berryteuthis anonychus (Pearcy & Voss, 1963)

The Gonatidae are one of the most abundant oegopsid squid families in California waters. Two specimens of *Berryteuthis anonychus* (26, 72 mm DML) were captured in the midwater trawl fished between 400 and 500 m at night. This record adds another gonatid to these waters and extends the known range of *B. anonychus* southward from Oregon, the only other reported capture locality (PEARCY & VOSS, 1963; YOUNG, 1972).

Gonatus californiensis Young, 1972

Published eastern North Pacific ranges of *Gonatus* species are from northern Baja California to off Oregon

(YOUNG, 1972; PEARCY *et al.*, 1977). A single specimen of *Gonatus californiensis* (15 mm DML) was taken in the same haul as the *Berryteuthis* specimens, and represents the northernmost record for this species. Also, a single

Gonatus berryi Naef, 1923

specimen of *Gonatus berryi* (20 mm DML) was taken in the midwater trawl between 400 and 500 m at night. Another *G. berryi* was taken in a zooplankton tow fished to 200 m at night but subsequently was lost.

Gonatus onyx Young, 1972

Larval and juvenile *Gonatus onyx* were the most abundant pelagic cephalopod taken in midwater trawls in Monterey Bay (72 specimens, 8-53 mm DML). An upward shift at night for these young was evident (Figure 3). Three spec-

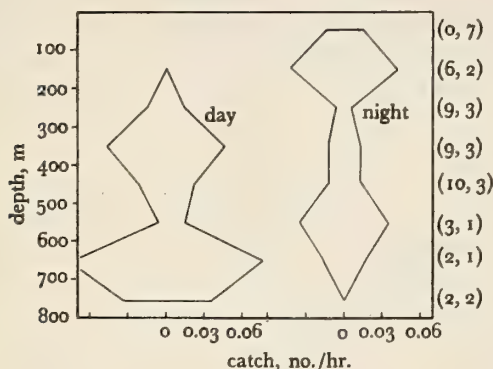


Figure 3

Vertical distribution of *Gonatus onyx* in Monterey Canyon. Catch per effort mirrored. Numbers in parentheses on right are sample sizes in each 100 m interval, day first, then night

imens (42-45 mm DML) were dip-netted at the surface one night. Although hauls below 500 m were scarce, an increase in number occurred around 600 to 700 m during the day, possibly due to a near-bottom concentration of nekton and plankton noted for some fish and crustaceans as well (ANDERSON, 1977). ROPER & YOUNG (1975), by using a correction factor to compensate for unequal trawling time at depth, show the daytime center of abundance of the species in southern California waters to be around 600 m. PEARCY *et al.* (1977), however, show a daytime center at about 300

m off Oregon with small individuals clustered in the upper 100 m. LU & CLARKE (1975) suggest a pattern of ontogenetic descent (larvae descend as they grow) in *G. fabricii* which, if applied to *G. onyx* in Monterey Bay, would mean the proposed vertical migration in this species is a compounded result of different distributional patterns.

Gonatopsis borealis Sasaki, 1923

Two young *Gonatopsis borealis* (22, 26 mm DML), a species ranging from California to the Bering Sea and Japan, were taken in the same midwater trawl haul as the *Berryteuthis* specimens in 400 to 500 m at night. In addition, two large adults (229, 185 mm DML) were taken in a commercial trawl operated by the National Marine Fisheries Service off Santa Cruz in August, 1976. This daytime collection in nearshore waters of 220 to 250 m depth probably is unusual, unless adults occupy shallower water than juveniles. PEARCY *et al.* (1977) found the daytime distribution of young *Gonatopsis* in oceanic waters off Oregon to be between 200 and 600 m. Similarly, ROPER & YOUNG (1975) found the daytime center of distribution off southern California to be about 400 to 600 m for this species.

ONYCHOTEUTHIDAE

Moroteuthis robusta Verrill, 1876

Five records of the giant squid, *Moroteuthis robusta*, exist from Monterey Bay (BERRY, 1912b, 1914; PHILLIPS, 1933, 1961; SMITH, 1963). HOCHBERG (1974) reported some recent captures from southern California and SMITH (1963) and TALMADGE (1967) have reported captures from northern California. One larval specimen (26 mm DML) that is tentatively referred to this species (R. E. Young, pers. comm.) was taken in the midwater trawl fished at night in 400 to 500 m. Additionally, an immature female 710 mm DML was found floating dead at the surface by MLML divers about one mile off Moss Landing. Apparently, the species is abundant in about 200 to 400 m, particularly during the fall.

Onychoteuthis borealijaponicus

Okada, 1927

Onychoteuthis borealijaponicus is represented in the collection by four larvae (9-16 mm DML) taken at night in 400 to 500 m. Adults periodically are common at the surface just outside the bay and often are taken by local fishermen for bait.

CHIROTEUTHIDAE

Chiroteuthis calyx Young, 1972

Six specimens of *Chiroteuthis calyx* (26-52 mm DML) were taken in the midwater trawl fished between 300 and 700 m. Other cruises have yielded additional specimens bringing the present total to 21, and the species apparently is abundant year-round. All specimens are "doratopsis" larvae or young juveniles less than 70 mm DML. One larva (31 mm DML) was dip-netted at the surface at night.

Valbyteuthis danae Joubin, 1931

A single specimen of *Valbyteuthis danae* (55 mm DML) was caught in the midwater trawl at night in 400 to 500 m. YOUNG (1972) also reported a single specimen from off southern California and concluded his specimen was a straggler from a more tropical population, since previously it was known only from Panama and Peru. CLARKE & LU (1974) suggested ontogenetic descent in this species, and indeed YOUNG (1972) described it as one of the deepest living cephalopods off southern California. This second California specimen suggests the species is more widely distributed than current data indicate.

CRANCHIIDAE

Galiteuthis phyllura Berry, 1911

Larval and juvenile *Galiteuthis phyllura* were the second most abundant cephalopod sampled by midwater trawl (36 specimens, 6-68 mm DML). A slight upward shift at night was detected for these specimens and the species was absent from the upper 100 m (Figure 4). ROPER & YOUNG (1975)

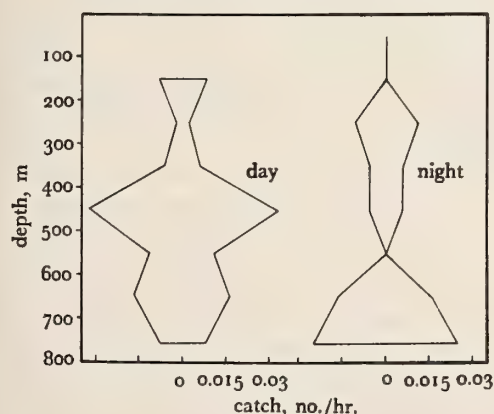


Figure 4

Vertical distribution of *Galiteuthis phyllura* in Monterey Canyon.
Graphics after Figure 3

show ontogenetic descent in larval *Galiteuthis*. Only five specimens larger than 60 mm DML (larval development complete) were taken in the bay and these were from night tows between 300 and 600 m.

VAMPHYROMORPHA

VAMPHYROTEUTHIDAE

Vampyroteuthis infernalis Chun, 1903

A single young specimen of the vampire squid, *Vampyroteuthis infernalis* (13 mm DML) was taken in an open midwater trawl that fished to 1000 m by personnel of Hopkins Marine Station, Pacific Grove. An inhabitant of great depths, it is likely that more specimens will be taken in the bay as deeper hauls are made, since it is considered a worldwide species (PICKFORD, 1946).

PHILLIPS (1934) reported a specimen of *Cirrotheuthis macrope* Berry, 1911 from the bay but this nominal species should be referred to the synonymy of *Vampyroteuthis infernalis* Chun, 1903 (YOUNG, 1972). It is not known if Phillips' specimen was a vampire squid or a cirrate octopod such as *Opisthoteuthis californiana* which it resembles. The specimen could not be found and may not have been preserved.

OCTOPODA

BOLITAENIDAE

Japetella heathi (Berry, 1911)

Two young specimens of *Japetella heathi* (13, 27 mm DML) were taken by the closing trawl in daytime tows between 300 and 600 m. Two other specimens (17, 21 mm DML) were taken in open nets fished to over 500 m during the day. YOUNG (1972) indicated some taxonomic confusion exists in *Japetella* and the Monterey Bay specimens have been tentatively identified to *J. heathi* due to the presence of silvery tissue around the eyes.

ARGONAUTIDAE

Argonauta pacifica Dall, 1872

The tropical-subtropical paper nautilus, *Argonauta pacifica* has been found off California, apparently more often during warm water years of the nineteenth century. DALL (1872: 95) first reported it, "so common at certain periods on the coast of California . . ." and later listed it from Mon-

terey Bay (DALL, 1908). Apparently, it has not been collected subsequently in the bay.

OCTOPODIDAE

Graneledone sp.

Four specimens of the slope-dwelling octopod, *Graneledone* sp., recently were taken off Monterey Bay. One, from a commercial sablefish trap set in 1165 m, measured 156 mm DML. Three others (100, 108, 121 mm DML) were taken in a beam trawl at depths of 1336 to 1409 m. During

Benthoctopus sp.

the same cruises, 4 specimens of *Benthoctopus* sp. (34, 35, 41, 50 mm DML) were caught in hauls made between 1336 and 1609 m. Neither species has been positively identified and they may be new to science (W. G. Pearcy, pers. comm.).

Octopus californicus Berry, 1911 ?

Octopus dofleini (Wülker 1910)

Octopus leioderma Berry, 1913

Octopus pricei Berry, 1913

Octopus rubescens Berry, 1953

Three species of *Octopus* are known to me from recent collections in the bay: *O. rubescens*, *O. dofleini* and *O. leioderma*. BERRY (1911, 1912a) listed a young *O. californicus* from deep water off Monterey Bay but cautioned that its identity was not certain. *Octopus pricei* was described from Monterey Bay (BERRY, 1913), but no individuals positively referable to this species have been identified recently. *O. rubescens* is the commonest intertidal-subtidal octopod in Monterey Bay (see WARREN *et al.*, 1974; BALLERING *et al.*, 1972) and it has been taken to a depth of 267 m. Below that depth *O. californicus* should occur, but collections from the canyon at depths greater than 200 m are few and specimens have not been obtained as yet. PHILLIPS (1934) reported *Polypus hongkongensis* as the common subtidal octopod that composed most of the California fishery. PICKFORD (1964), however, showed *P. hongkongensis* BERRY, 1911 to be a synonym of *Octopus dofleini* (Wülker, 1910), a widely distributed, variable species. Additionally, a recent otter trawl collection in the bay yielded 2 specimens of *Octopus leioderma* (45, 55 mm DML) from 110 to 149 m depth.

OPISTHOTEUTHIDAE

Opisthoteuthis californiana Berry,

1949

A single, bright orange juvenile of the benthopelagic octopod *Opisthoteuthis californiana* (21 mm DML) was taken in the midwater trawl at a depth of 350 to 460 m (between 120 and 260 m above the bottom) during the day. This specimen lived for 5 days in the Steinhart Aquarium cold water tank at MLML (see MCCOSKER & ANDERSON, 1976). The octopod exhibited positive phototaxis (in dull light) and swam in short bursts by rapidly pulsing its webbed arms, augmented by siphonal jet propulsion. The fins were flapped alternately to maintain a vertical position in the water column in the manner reported by PEREYRA (1965).

DISCUSSION

Although the collection of pelagic cephalopods reported here lacks a total size range for all species and, in fact, represents only a few specimens of each, it is the largest series of its kind collected so far from Monterey Bay. To emphasize the prior lack of knowledge of cephalopods from this area, it should be noted that a single haul of the Tucker trawl one night yielded 5 species never reported before from the bay.

To examine seasonal variation in the pelagic cephalopod catch, numbers of species and individuals of cephalopods were compared to numbers of species and volumes of all micronekton (fishes, shrimp and squid) and plotted against time. The result was that cephalopod abundance remained almost constant due to the numerical dominance of *Gonatus onyx* and *Galiteuthis phyllura*. A one way analysis of variance with unequal sample size (SOKAL & ROHLF, 1969) showed that variability in micronekton volumes was so high within seasonal categories that differences were not statistically detectable. This was thought to be due to small sample size, variability in depths sampled and the rather weakly defined hydrographic seasons in Monterey Bay during the trawling (BROENKOW *et al.*, 1975, 1976).

However, PEARCY (1976) recorded an increase of nekton and plankton in the winter in nearshore areas off Oregon. Similarly, FAST (1960) showed a winter "invasion" of juvenile lanternfish, *Stenobrachius leucopsarus* in Monterey Bay and hypothesized that at this time of year the canyon may act as a concentrating basin in conjunction with the nearshore component of the northward flowing Davidson

Current. At this time, the effect of nearshore submarine canyons on the concentration of nekton and plankton is unproven and clearly more study is needed in this area.

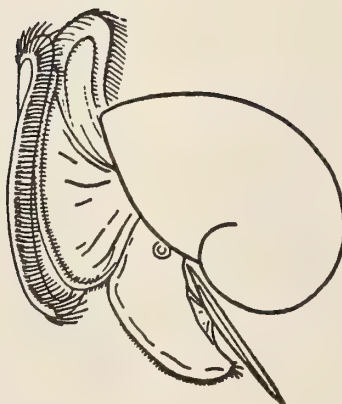
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Antipredator Behavior in *Octopus dofleini* (Wülker)

BY

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THE GIANT PACIFIC OCTOPUS, *Octopus dofleini* (Wülker, 1910), is a large and active predator in the marine subtidal. In spite of its own predaceous habits the octopus itself is a victim of attacks by a variety of other predators including seals (KENYON, 1965), sea otters (KENYON, 1975), dogfish sharks (BROCKLESBY, 1927), lingcod (Brian Francis, pers. comm.) and, of course, man.

During a study of the population ecology and behaviour of *Octopus dofleini* on the west coast of Vancouver Island, we recorded considerable evidence of predation on these organisms. Of 39 octopuses weighing between 0.37 kg and 18.2 kg collected subtidally in Clayoquot Sound, 66% had considerable scarring and 50% had partially amputated arms. This evidence along with reports from local divers who observed unidentified fish attacking a medium-sized octopus (Harley Regan, pers. comm.) suggests that octopuses are not the top carnivores that they would seem to be.

As PACKARD (1963) and others (see for example, YOUNG, 1958) have suggested the octopus is an animal which has a den for a base which it leaves to attack prey, and into which it withdraws if disturbed. The behaviour of an octopus can then be interpreted in terms of visual responses involving an approach response and a withdrawal response (PACKARD, 1963). Packard gives the components of these responses for *Octopus vulgaris* as well as providing an interpretation of other behaviour patterns including a sucker display, as responses lying along an approach-withdrawal axis. Although species like *O. vulgaris* have been well-studied, especially in the laboratory, similar observations are lacking for *O. dofleini* and reports on their behaviour in their natural environment are almost non-existent. After KYTE & COURTNEY (1977) reported their observation of aggressive behaviour in *O. dofleini*, we attempted to compile our own observations on this animal. We have approached octopuses of various sizes in the dens and in the open; in some cases just to clear shells from a den and at other times to actually remove the octopus in an experimental harvest program.

During our studies of *Octopus dofleini* we have checked many dens. The octopus inhabiting a den usually observes our activities around the den entrance with one eye only.

In some cases one arm would uncurl out toward a diver and then withdraw back into the den. Aggressive encounters were rare but several are reported later in this paper. In one case an octopus weighing approximately 2 kg was sufficiently disturbed by our collecting of shells at the den, to jet quickly away only to settle about 5 m above the den where it remained motionless. Moving away quickly or remaining motionless are two responses observed in *O. dofleini* and reported commonly in species like *O. vulgaris*. PACKARD (1963) describes the components of the withdrawal response of *O. vulgaris*. The head is depressed, the body blanched except for darkening around the eye and suckers, and the arms are curved back and upward. The funnel is directed at the stimulus. In our encounters with *O. dofleini* the octopus if approached in the open would usually remain cryptic and motionless as long as the diver remained some distance away. If this reactive distance was breached then the animal would flee. The distance at which an animal reacts by fleeing varied from a meter to almost nil. In one case an octopus estimated to be 4.5 kg was found in the open and it remained motionless even when the mantle was caressed. Numerous papillae were raised, however.

Some of our best observations of antipredator behaviour have arisen during the experimental harvesting project. In each case an occupied den had bleach squirted into it. The divers would then move off behind rocks to await emergence of the octopus. Puffs of silt from the den opening indicated that the animal was about to emerge. The octopus leaves the den and stops a meter or so outside. On seeing the divers the body of the octopus moves quickly down in what appears like a "ducking" movement. Since the octopuses view the diver with one eye only this movement may give some estimate of distance. With the first bob, the animal blanches. The whole body pales including the area around the eyes; unlike *Octopus vulgaris* which darkens the area around the eyes. The octopuses then spread their interbranchial webbing in one fluid motion by thrusting the arms out and backward although the tips are kept curled in close to the body. The octopus remains immobile in this position for several seconds after which it moves quickly back into the den

or some other nearby hole if possible. If a den or hole is not accessible, the octopus swims up and away, often ejecting ink directly at the diver. An octopus that has settled on the bottom after being chased has prominent horns behind the eyes and swollen papillae on its mantle.

The dramatic display described above presumably startles a potential predator and permits the escape of the octopus. Interestingly the display had this effect on the divers at least in the first few instances and actually enabled the animals to escape. Often the octopus would retreat quickly back into its den immediately after the display. The display certainly gives the animal an appearance of much larger size. Small octopuses did not give a complete display. Although they became pale, they did not extend their arms and usually they were very quick to flee. Such a response would seem appropriate for animals which would be relatively small even in full display.

Although HIGH (1976) suggested that the behaviour of *Octopus dofleini* was unpredictable, the observations we have made indicate predictable responses under certain circumstances.

We did not observe any sucker displays in *Octopus dofleini*. The sucker display described in *O. vulgaris* by PACKARD (1961) is presumed to be an intraspecific display. A photograph of *O. dofleini* in High's paper shows some resemblance to this display but no other evidence exists. However, measurements of maximum sucker size on arms of 39 specimens of *O. dofleini* indicate that the largest suckers in males are proportionately larger than those in the female (HARTWICK, 1977) and it may be that such a display is used during mating activities.

In addition to the withdrawal display described earlier, octopuses show a particular attack or approach response. PACKARD (1963) describes this for *Octopus vulgaris* as a deep brownish-reddening of colour combined with orientation changes. We observed an octopus in the open and holding a crab; the colour of the octopus appeared as deep brown. KYTE & COURTNEY (1977) described a similar mottled reddish-brown colour for an octopus attacking another octopus; the opponent appeared blanched. Although we have not seen any aggressive encounters between octopuses we have had such interactions with the animals ourselves. On October 24, 1976, two divers descended to a den located at 18 m. Two large octopuses were present, one just inside the den, the other in front of the den. The one in front on seeing the divers several meters away moved up off the bottom spreading its webbing and arms and taking on a dark brownish appearance. It then moved toward the divers and in fact kept advancing even when the divers had retreated to a ledge at 10 m. On Nov. 2 both octopuses were present inside the den

which was actually a horizontal crevice. When we started to collect shells near the den one octopus moved out of the den towards us but stopped several meters away and then moved back into the den. On February 11, 1977 a light was shone into the same den which now held only one large octopus estimated to weigh 20 to 30 kg. The octopus came directly out at the divers and when emerging had an almost black colouration. Once out of the den, the octopus swam about 1 m above the den in a single burst and extended all 8 of its arms; an unusual case since whenever we had encountered other octopuses in mid-water their reaction was to flee immediately leaving behind a trail of ink. No paling was observed by the divers and when the octopus settled to the ledge in front of the den its colour appeared totally black or very dark brown. The octopus then crawled toward the divers. Such aggressive encounters are of great interest. The battle observed by KYTE & COURTNEY (*op. cit.*) occurred in January and may have been related to reproductive activities or territoriality during the mating season. Although we have no evidence of territoriality in *O. dofleini*, their general level of aggression may be higher in late fall and early winter which is presumably the normal mating period. In fact, commercial divers (Rod Palm, pers. comm.) have reported a much higher frequency of attacks during this time.

The full significance of this and other behaviour patterns in *Octopus dofleini* will only be understood through continued recording of observations of their behaviour in the natural environment.

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Mating Behavior of *Octopus joubini* Robson

BY

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INTRODUCTION

OBSERVATIONS ON THE SEXUAL BEHAVIOR of octopuses have been made for nearly 100 years; however, most studies have examined one or several matings of a single pair of animals in an aquarium. YOUNG (1962) was one of the few investigators who observed mating in the field, and he described only a single instance. Earlier workers debated whether the mating behavior of *Octopus vulgaris* is "violent" (the male holds the female forcibly) (KOLLMAN, 1876) or "peaceful" (there is no restraint and contact is only by the male's extension of his third right arm or hectocotylus) (RACOVITZA, 1894). VON ORELLI (1962) and WODINSKY (1973) noted both types of approach in *O. vulgaris*. However, in other species, *Haplochalaena maculosa* (TRANter & AUGUSTINE, 1973), *Eledone cirrhosa* and *E. moschata* (VON ORELLI, *op. cit.*) only "violent" mating was observed. These types of mating may be species-typical, but they are more likely affected by manipulations in moving and confining the animals (for instance, if they are territorial they will behave differently in their own territory than in another animal's).

While observations have shown a great variety in mating behavior, recent research has outlined some of the behavioral units that appear to be components of normal mating in at least a few octopus species. WELLS & WELLS (1972) described the Arch and Pump movement by which spermatophores are inserted through the siphon into the tubular fold along the male's third right arm (hectocotylus), and thus passed to the female. WODINSKY (1973) described a rise in the respiration rate of the female during copulation which he attributed to the contact of the male's hectocotylus with the female's oviduct prior to spermatophore passage. The present report makes use of these units of sexual behavior to describe mating in *Octopus joubini* Robson, 1929. Because *O. joubini* is very small, it was possible to confine several animals in a large tank without excessive crowding and create a fairly natural situation. Because few matings

were observed in this situation, octopuses were also isolated and paired repeatedly with the same animals in the smaller tanks. These two procedures allowed observations in both a near-normal and a controlled situation, and make it possible to describe mating behavior in terms of number of Arch and Pumps, duration of mating, sex of initiating animal, and rise in respiration of female.

METHODS

I. "Semi-Natural" Observations: Six *Octopus joubini* (3 males, 3 females) collected from St. Joseph Bay, Florida, and flown to Boston, were confined in a plexiglass tank measuring 1 m × 1 m × 30 cm and filled with 180 L sea water (to approximately 18 cm), and were in captivity for 2 months before the observations. Plexiglass cube "homes" (2.5 cm cubes with 4 dark sides, one open, and one clear for observation) were provided so the animals could hide during the day. Constant lighting was provided by a dim red light overhead; during the day additional lighting was provided by a white lamp beside the tank. This lamp was controlled by a timer set to the normal Boston day length and was corrected every 2 weeks. The octopuses were fed 12 *Uca* sp. fiddler crabs every 2 days (1 crab/octopus/day) from August until mid-November, when prey was changed to *Nassarius* sp. mud snails because the *Uca* were no longer available (but the schedule was unchanged). No attempt was made to feed individual animals, but all were observed eating several times. Temperature was maintained at or near 25°C (± 1°), salinity was monitored and corrected weekly, and 72 L of water was changed every second week to prevent the accumulation of nitrates. Observations were made without a blind because after the animals had been repeatedly exposed to the experimenter sitting quietly in a chair, they ceased to respond and were disrupted only by abrupt motion. *Octopus joubini* is strongly nocturnal, so all observations were made in the evening, at least 2 hours after sunset,

between 1900 and 2400 hours. Observations were made in November and December when all animals were physically mature. When a pair of octopuses mated, preceding behavior was noted, female respiration rate rise observed, Arch and Pumps counted, and relative positions of the animals described.

II. Pairing Observations: (a) **Housing**—Ten additional octopuses were isolated for pairing experiments. Between matings they were kept in 18 L- or 36 L-capacity aquaria that were maintained at 25°C ($\pm 1^\circ$) with salinity corrected weekly and $\frac{1}{3}$ of the water changed weekly to prevent accumulation of nitrates. Lighting was provided by a dim red overhead light at night and white room lights during the day, timed to the normal Boston day length and adjusted weekly. Plexiglass "homes" (5 cm cubes with 2 ends transparent, 4 sides dark, with one of these half cut away to allow passage) were provided for the octopuses. Each octopus was offered 6 *Uca* fiddler crabs daily (an average of 1 - 2 were actually eaten).

(b) **Pairing**—The 10 octopuses were grouped into 5 pairs. Originally 10 matings per pair were planned, but the sequence could not be completed for every pair because 3 of the females laid eggs in early January. To minimize variation, the same male was always paired with the same female, after a constant deprivation time of 4 days.

Pairings were made in 2 modified 18 L-capacity aquaria that were surrounded by an opaque plastic shield containing small observation slits. Octopuses were brought to one of the observation tanks in their "homes" and eased out, with the aid of a pencil if necessary. The female was brought out first, then the male; until the onset of observations 1 minute later the animals were kept separated by a transparent plexiglass partition. Until mating was initiated, the animals were observed through the peepholes, then the front panel of the blind was folded back to allow viewing (octopuses are not easily disturbed when they are mating). Since *Octopus joubini* are nocturnal, matings were initiated during their active period, between 2100 and 2400 hours. Octopuses were left in the tank 30 minutes after their mating to ensure that they had finished (a single exception was made when a large female cornered and attacked a small male). Observations were dictated into a portable tape recorder and later transcribed. The number and spacings of Arches and Pumps, presence of an increase in female respiration rate, initiation, termination and duration of mating, and relative position of the octopuses were recorded. Females expelled spermatophores during mating and this evagination process was observed carefully.

RESULTS

Thirty-two matings were observed in the pairing situation and 6 in the semi-natural situation.

(a) **Duration:** Matings were nearly always brief; the mean duration for all matings was 5.4 min. (5.0 min. for pairings and 6.5 min. for semi-natural) (Table 1).

Table 1

Some Characteristics of the Mating Behavior
of *Octopus joubini* Robson

Factor	Repeated Pairings (n = 32)	Semi-Natural Situation (n = 6)
Duration	5.0 min (Range 2-28 min)	6.5 min (Range 4-9 min)
Number of Arch and Pumps	1.8 (Range 1-13)	2.3 (Range 2-3)
Female Respiration Rise	59%	100% (n = 5)
Sex of Initiator	Male = 19% Both = 9% Female = 72%	Male = 84% Both = 16%
Sex of Terminator	Male = 12% Both = 25% Female = 63%	Male = 33% Female = 66%
Mating Position	Close contact = 94% Distance = 6%	Close contact = 50% Distance = 50%

(b) **Arch and Pumps:** Few Arch and Pump motions were observed, an average of 1.9 (1.8 for pairings, 2.3 for semi-natural) (Table 1). The average interval between Arch and Pumps was also brief, 1 - 3 min. (1.3 min. for pairings, 1.4 min. for semi-natural). This feature of copulation was very stable, with a range of 0.33 to 5 minutes, but over half (29/48) at 1 minute.

(c) **Mating Initiation and Termination:**—The pairing and semi-natural situations differed in the amount of contact made when mating was initiated. In the semi-natural situation, 3 matings (50%) began with the male simply probing the female's home with his hectocotylus. Only 6% of the matings in the pairing situation were initiated in this fashion. The availability of homes in the semi-natural situation may account for this, and the higher percentage of male initiation of mating (83%, compared to 41% in the pairings). Termination of mating

was more uniform, being initiated normally by the female, 66% of the time in the semi-natural setting and 63% of the time in the pairing situation (Table 1).

(d) **Respiration Rate:** An increase in respiration rate was observed in 5 matings in the semi-natural situation (in the other, the female was only partly visible) for 100%, but only in 59% of the pairings.

(e) **Mating Position:** Nearly all (94%) of matings in pairings were with close contact, but only 50% of the matings in the semi-natural setting were in this position.

DISCUSSION

Despite the small number of matings observed in the semi-natural situation, it is worthwhile to contrast them with the matings in the pairing situation because copulations under relatively natural conditions have rarely been described for octopuses. Some aspects of mating such as number of Arch and Pump motions, Inter-Arch-and-Pump Interval, and total duration of mating appear stable. But other aspects, such as amount of contact during mating, and sex of the octopus initiating and terminating mating, seem to be more variable and may be influenced by the experimental situation. Most pairing matings were in close proximity but most semi-natural ones were not; this confirms WODINSKY's (1973) and VON ORELLI's (1962) conclusion that no one contact pattern is species-typical for any one octopus species. VON ORELLI (*op. cit.*) ascribed differences in mating procedure both to relative size of the animals and to female behavior; in *Octopus joubini*, it may also be affected by the space and homes available to the female. For example, if one animal is in its home tank then it may be more likely to initiate mating (WELLS & WELLS, 1972, for *O. vulgaris* and *O. cyanea*). The initiation of mating by female *O. joubini* in the pairing situation, which was not seen in semi-natural situations, may be related to the female being placed in the mating tank before the male.

Octopus joubini matings are very short (5 minutes) when compared with those of other *Octopus* species. *Octopus dofleini* copulated 2 - 3 hours (MANN, MARTIN & THIERSCH, 1970), *Haplochlalaena maculosa* 1 hour (TRANter & AUGUSTINE, 1973), and *Eledone* up to an hour (VON ORELLI, 1962). Short matings, and thus a short period of vulnerability, would be adaptive for a small (15 - 20g) octopus that is vulnerable to many predators (*Haplochlalaena* is small, but deadly venomous). Nevertheless, short mating duration may impede one aspect of reproduction. Octopus sperm are passed to the female in a

spermatophore that evaginates in the female's oviduct, depositing sperm in the oviducal gland. Normally the male holds the spermatophore in the female until evagination is completed, one hour for *O. dofleini* (MANN, MARTIN & THIERSCH, *op. cit.*) 1½ to 3 min. for *O. vulgaris* (DREW, 1919). However, male *O. joubini* cannot hold the spermatophore until evagination because this process takes too long. Evagination of loose spermatophores takes approximately 20 minutes, much longer than a total mating. Apparently in *O. joubini* the spermatophore may be kept in the oviduct by a mechanical process; for example, in loose spermatophores the anterior portion of the casing swells up like a bulb within 5 minutes after contact with sea water. Such an action would maintain the spermatophore in the oviduct and provide for both short matings and longer transfer times for sperm from the spermatophore.

These observations suggest that some aspects of mating, such as Arch and Pump movements, may be stereotyped in occurrence and common among octopods. Others, such as mating duration and position, may be more labile within and among species, and more affected by experimenter manipulation.

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Growth in the Keyhole Limpet *Fissurella crassa* Lamarck

(Mollusca : Archaeogastropoda)

in Northern Chile

BY

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(5 Text figures)

INTRODUCTION

AMONG THE SPECIES OF MOLLUSKS commercially exploited for food in the Iquique region. Chile, the keyhole limpets of the genus *Fissurella* Bruguière, 1789, collectively called "lapas," are important. The various species of *Fissurella* are often eaten instead of *Concholepas concholepas* (Bruguière, 1789) because this last species is diminishing due to intensive exploitation. *Fissurella* species are not protected by laws preventing small specimens to be collected and eaten, in spite of the great predation exerted on them by man.

In order to manage adequately or control a population, growth rate must be determined. However, there is little information on growth rate of commercially important Archaeogastropoda, SAKAI (1960), LEIGHTON & BOOLOOTIAN (1963), and WRIGHT (1976) have carried out studies on growth rate of *Haliotis* species, but we have not found data concerning growth rate of *Fissurella* species. *Fissurella crassa* Lamarck, 1822, locally called "lapa desol," was chosen for the present study because it has been one of the most exploited species of the genus.

MATERIALS AND METHODS

The specimens selected for this study lived between the *Chthamalus* and *Lessonia* belts throughout the rocky intertidal area in front of the Laboratorio de Ecología Marina, Universidad del Norte (LEMI), at Huayquique, Iquique,

Chile (20°17' S, 70°08' W). They were marked and measured individually after being gently removed.

Animals were marked in three ways: (1) Small numbered tags were glued to the clean, dry shell and covered with Dekophane adhesive (Rona Pearl Inc., Bayonne, New Jersey). This method was not entirely satisfactory. Even when the glue set properly, epibiontic limpets (*Scurria parasitica* (ORBIGNY, 1841) sometimes grazed the numbers off, or algae and cirripeds set on the numbers, or the numbers became erased. (2) Small numbered tags were glued on the shell and covered with Revell cement (Revell, Ltd., Great Britain). This method was not more satisfactory than the former. (3) Serial notches were sawed near the apical orifice and on the shell margin. Growth did not greatly disturb the identification notches. The notches also were easily detected in recaptured animals. These marks persisted longer than the numbered tags, thereby providing the best way of marking, and were easily renewed when fading. Their influence on the physiology of shell growth was not evaluated.

The size of marked animals varied between 20 and 77 mm of shell length as initial size; specimens smaller than 20 mm were difficult to mark. Periodically new animals were marked during the first year until a total of 360 was reached. Animals which lost their numbered tags could sometimes be identified by their size, the quantity and position of their epibionts, and their position in the field. In such case they were retagged.

Growth was measured to 0.1 mm using vernier calipers. Shell length was usually measured once a month during low tides when wave impact was not strong. Length increments were standardized to: length increments per year = length increments X number of days between the first and

* This research project was supported by the Universidad del Norte Sede Iquique

last measurements/365 (WRIGHT, 1976). The relation between annual growth rate and age was established by using Walford's graphic (WALFORD, 1946). Growth rates (length increment/number of days between two successive growth measurements) were calculated for every marked animal. Mean growth rates of all size animals observed during the same period were calculated and plotted against time to detect seasonal growth variations.

Animals were measured for 19 months. The data presented below concern 88 animals which were measured for at least 100 days.

Monthly mean surface sea water temperatures at 8:30 and 15:30 hr were taken from the data records of the LEMI. The extreme temperatures registered during the study period were 13° and 24° C, respectively.

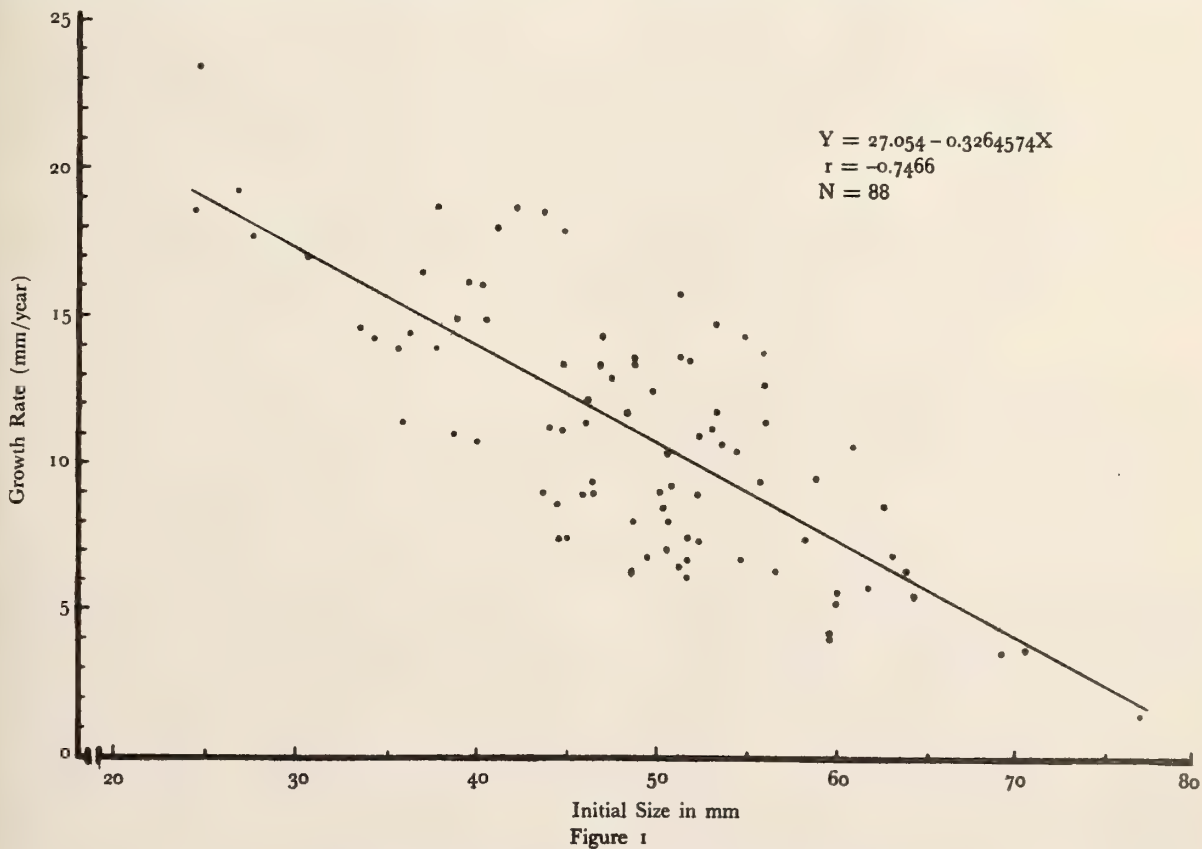
RESULTS

Of 360 marked individuals, 153 were never recaptured (42.5%); these comprised 42.9% of the animals bearing numbered tags and 38.9% of the notched animals. Of the remaining 207, only 88 (24.4% of the total) were recap-

tured from 3 to 15 times during the observation period, and 15 of which were measured for at least one year.

In the experimental rocky area *Fissurella crassa* feeds mainly on green algae such as *Ulva* sp. and *Enteromorpha* sp. It usually moves to feed when covered by sea water during high tides, at night, returning to home sites during diurnal low tides. A home site may neither be the same nor last for the whole life of a given individual. For instance, small animals (20-30 mm shell length) change their home sites more often than large sized specimens do. Moreover, some may return to the same rocky hollows from 1 to 6 months, but they usually migrate downwards to the *Lessonia* sp. intertidal and subtidal belt in spring. Others do not stay at the same site and at successive growth determinations were found at sites 0.6 to 20.0 m away from the last location observed. The individuals staying longer at their home sites were those living in clefts about 10 to 50 cm deep. One particular specimen has been observed for 15 months in the same cleft.

The growth rate for each studied *Fissurella* is presented in Figure 1. Growth rate was highly variable even for individuals of close or similar initial size (Figures 1, 2).



Growth rate for each *Fissurella crassa* measured for 100 days or more

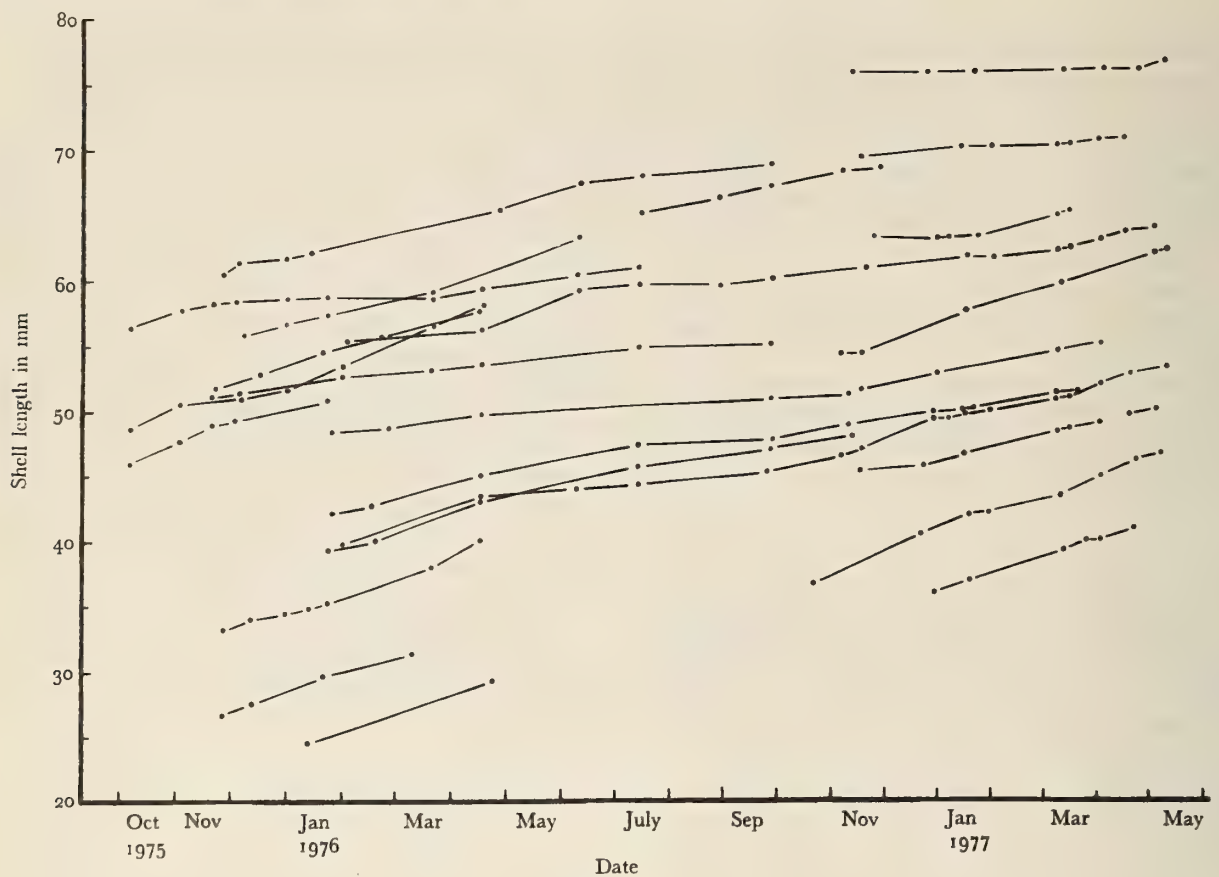


Figure 2

Individual growth of *Fissurella crassa* followed through the seasons
(23 individuals represented)

Fissurella crassa seems to exhibit a seasonal growth pattern. A rapid growth coinciding roughly with a period of rising temperatures was observed in spring (Figures 3, 4). The mean growth rate was diminished in late spring and early summer to values as low as those found in winter. This decrease is followed by an accelerated growth that declines again in late autumn. Low growth rates were recorded in winter months. It should be noted that the winter decrease in growth rate is a rather general feature of the *Fissurella crassa* population under study. Nevertheless, the low growth rate observed in December-January (Figure 4) corresponds to a mean value. Forty-one animals presented very little growth (under 0.01 mm per day) or no growth at all for a short period from November to April, the highest incidence of no growth occurring in January (Table 1). The rest of the animals showed diverse growth rates during that period.

Table 1

Frequency of Growth Rates Observed in
Seasons Different from Winter in
Fissurella crassa from 40 to 77 mm of Shell Length.

Month	Number of individuals	Growth Rate mm/day		
		Range	Mean	Stand. Dev.
November	5	0.0000-0.0081	0.0039	0.0028
December	11	0.0000-0.0071	0.0043	0.0028
January	13	0.0000-0.0083	0.0036	0.0030
February	6	0.0000-0.0090	0.0044	0.0034
March	4	0.0017-0.0076	0.0058	0.0023
April	2	0.0000-0.0088	0.0044	0.0044
TOTAL	41			

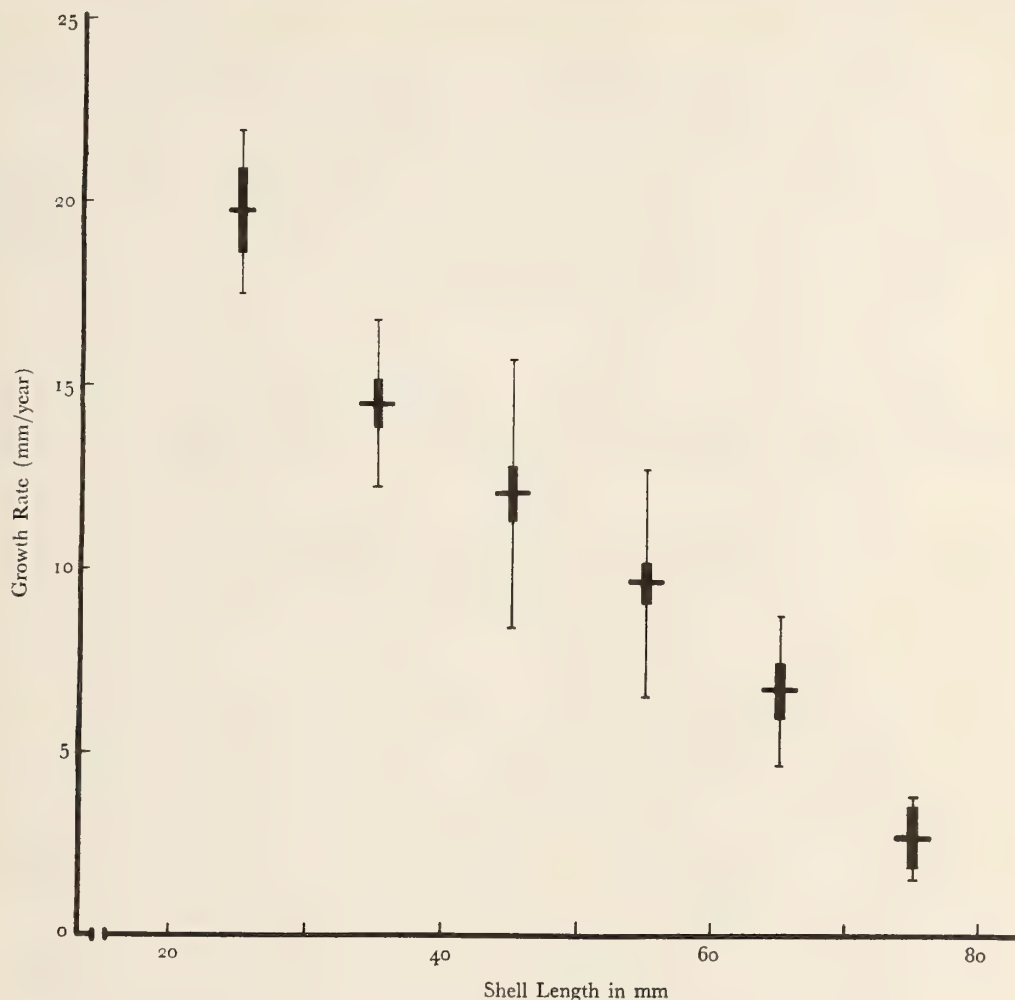


Figure 4

Mean seasonal growth pattern of *Fissurella crassa* at Huayquique

The mean growth rates for the different size classes indicate that growth would be 19.8 mm for the second year, 14.5 mm for the third, 9.7 mm for the fourth and 6.8 mm for the fifth. The usual commercial size of *F. crassa* is about 45-65 mm, although smaller specimens can often be observed in the market. If we assume that during the first year fissurellas grow to about 20 mm, commercial sizes should correspond to animals from 2 to 4 years old (Figure 5B).

According to Walford's graph (Figure 5A), maximum probable size for *F. crassa* is about 83 mm of shell length. This estimation agrees with reality since maximum size observed in Northern Chile for this species is 81.8 mm at present.

Twelve empty tagged shells were found in clefts in the study rocky area, probably left by predators. We cannot assume that this is the only real mortality of the population under study because its location in the field and the strong swell do not allow gathering every empty tagged shell.

DISCUSSION

Using notches to mark *F. crassa*, we failed to recapture 38.9% of the individuals. The loss of these animals could be attributed to death or to migration, probably to the surrounding subtidal zone.

Removing the animals to be marked and measured should not disturb them to make them move, since some

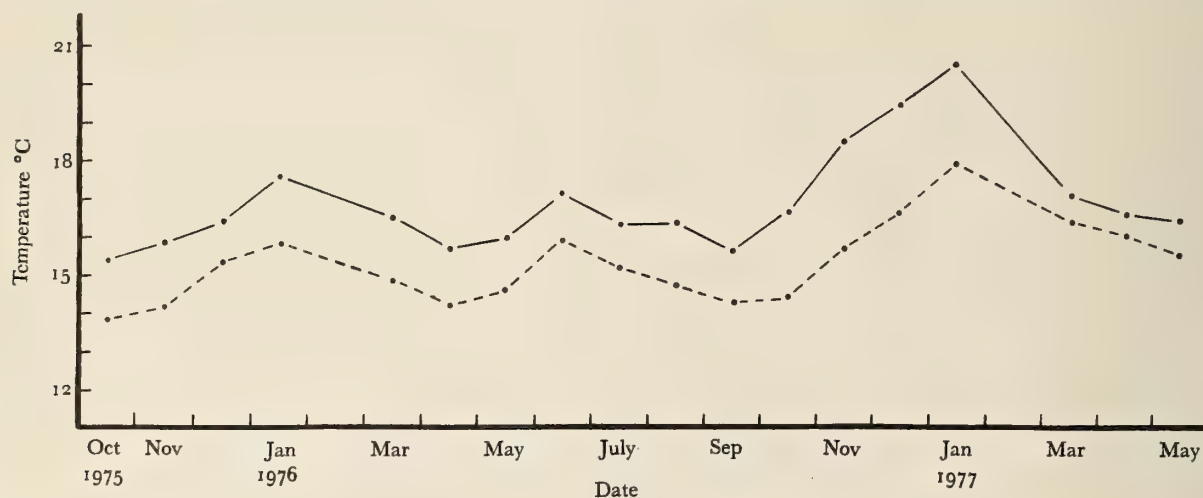


Figure 3

Monthly mean surface sea temperature at Huayquique.
Solid line represents temperatures at 15:30 hr; dotted line represents temperatures at 8:30 hr.

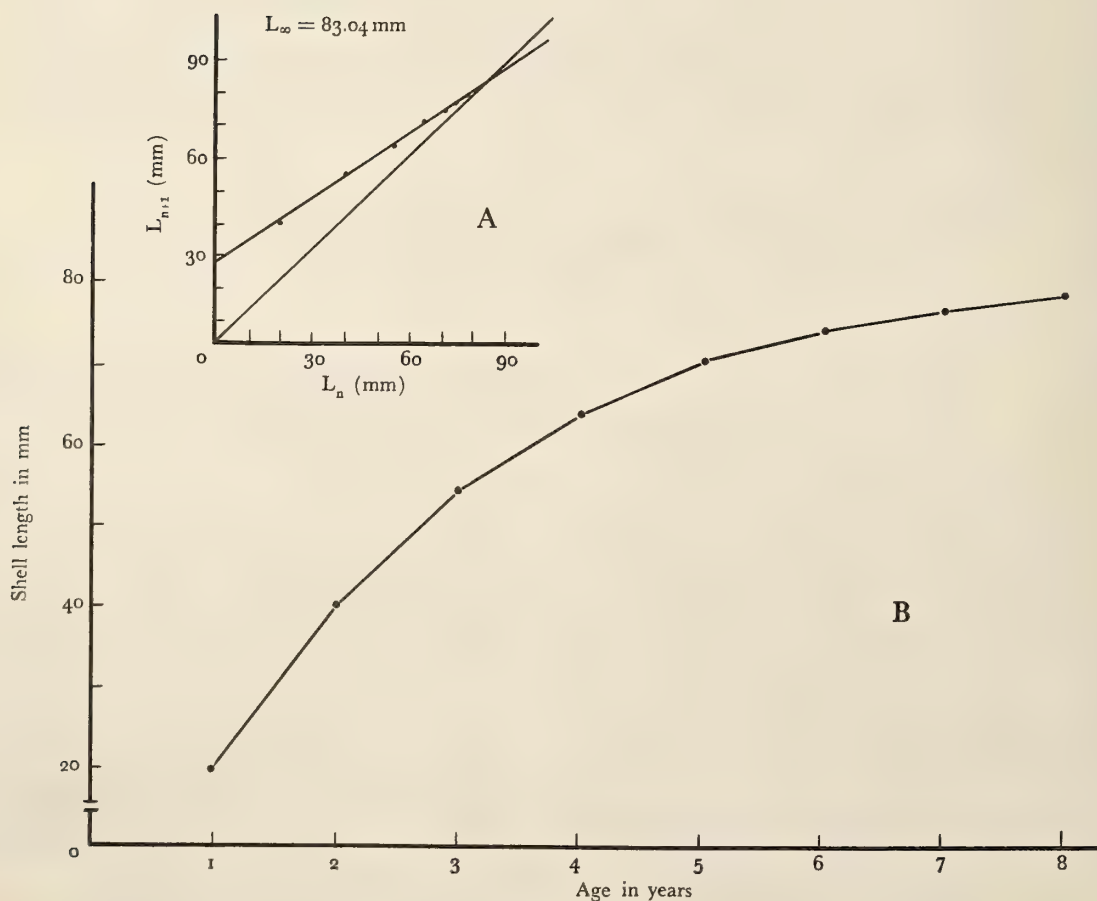


Figure 5

A. Mean growth of *Fissurella crassa* plotted according to Walford's method
B. Estimated age of *Fissurella crassa* at Huayquique

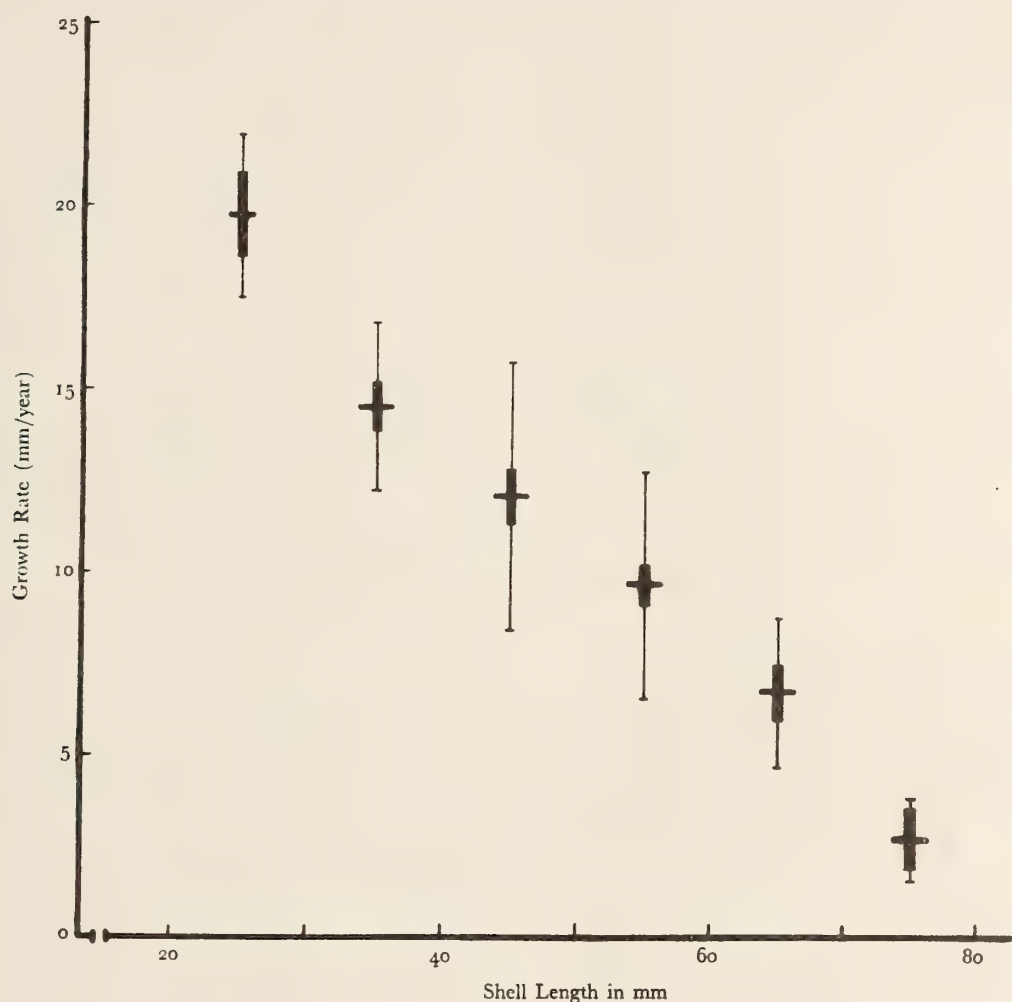


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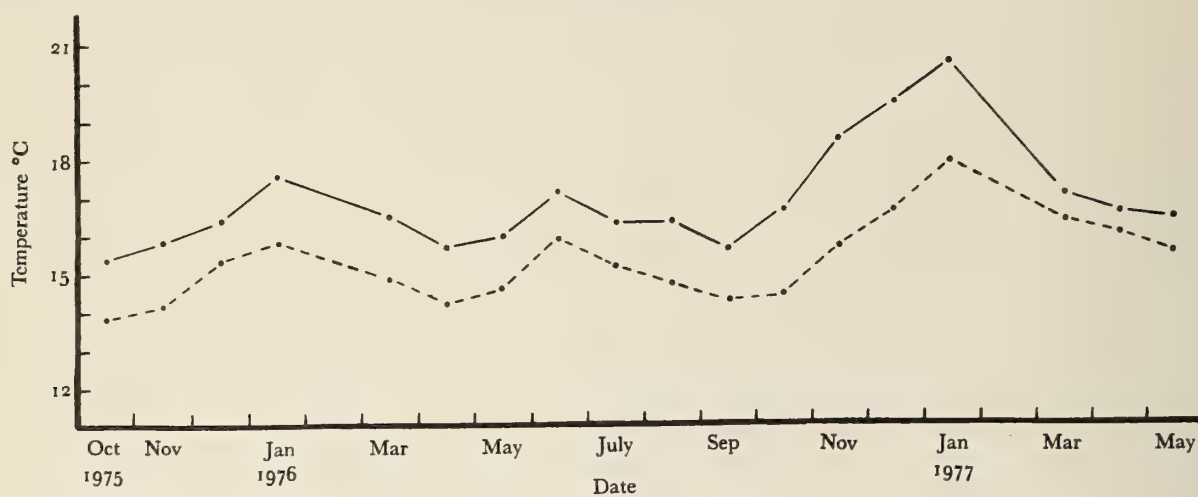


Figure 4

Mean seasonal growth pattern of *Fissurella crassa* at Huayquique

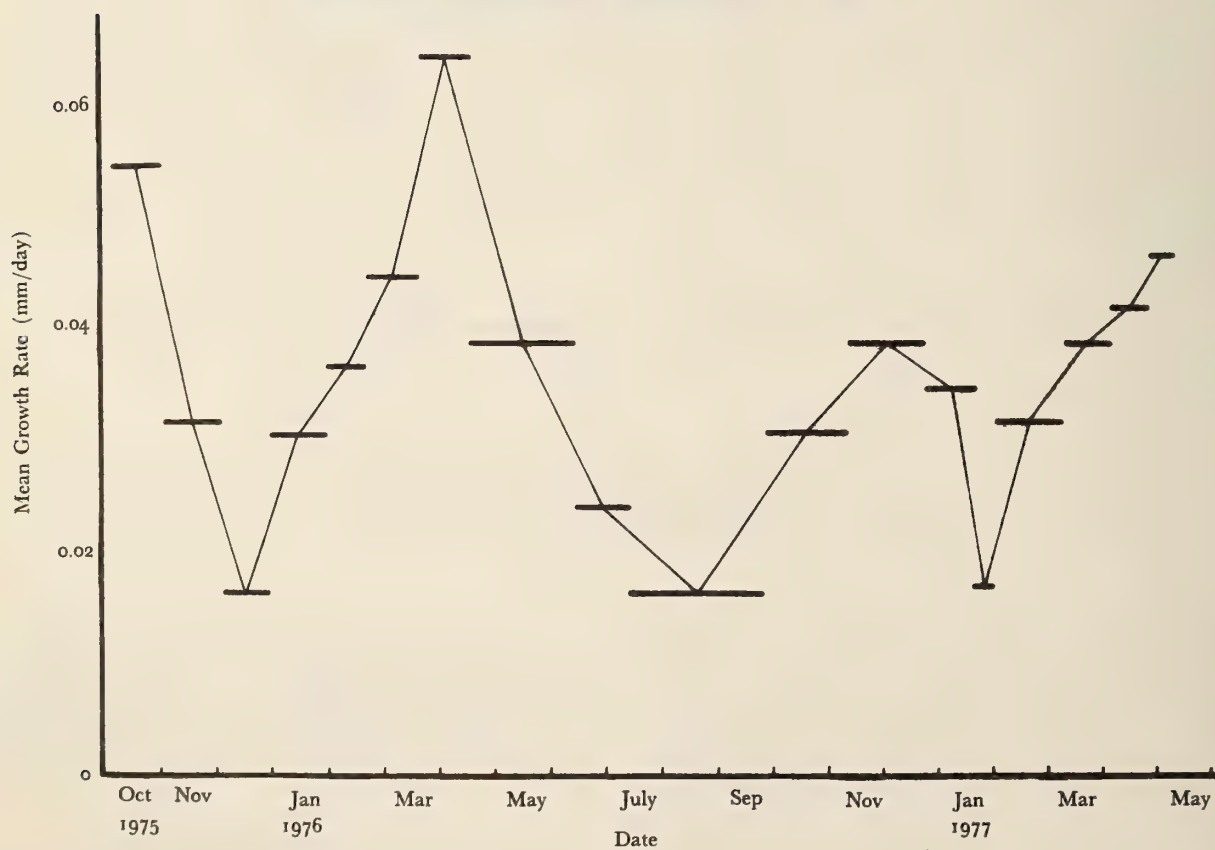


Figure 5

A. Mean growth of *Fissurella crassa* plotted according to Walford's method
 B. Estimated age of *Fissurella crassa* at Huayquique

of them, although repeatedly measured for a year or more, have always stayed at their home sites. Furthermore, animals used for growth studies which have been marked and measured *in situ* (WRIGHT, 1976) have immediately disappeared after having been marked or have not been found over successive measurement periods, as we have also observed in some individuals of *F. crassa*.

Great individual variations in growth rate among similar sized animals of the same species are a feature common to various gastropods, such as *Haliotis* (LEIGHTON & BOOLOOTIAN, 1963; WRIGHT, 1976), *Patella* (LEWIS & BOWMAN, 1975), *Acmaea* (FRANK, 1965), and *Purpura lapillus* (MOORE, 1938). This is the case with *Fissurella crassa*, too. These variations can be due to several factors. In Littorinid species some growth rate variations correspond to sex differences, females growing faster than males (BORKOWSKI, 1974). Since no external signs of sexual dimorphism are observed in *Fissurella crassa*, we could not detect sexual growth differences. Growth rate can also vary from one locality to another (MOORE, 1938; LEIGHTON & BOOLOOTIAN, 1963; BORKOWSKI, 1974) in relation with the food availability in each locality. MOORE (1938) observed that *Purpura lapillus* specimens feeding on different diets stopped growing at different sizes. HAVEN (1973) detected that a growth increase in *Acmaea* was accompanied by an algal upgrowth. In our study area home sites of *Fissurella crassa* are not identical and in different clefts diverse microclimates develop. Algae in the intertidal zone vary seasonally, so the food resources for *F. crassa* are also variable. It should be considered in addition that *F. crassa* in this area do not always stay at the same sites. Some individuals usually observed in winter in the intertidal zone between the *Colpomenia* and *Lessonia* belts migrate in summer downwards to lower clefts in the *Lessonia* belt and they can even be observed on rocks at 1 m below the extreme low water level. At this level *F. crassa* may have a different food supply and may compete for food with other grazers such as chitons, sea urchins and other species of *Fissurella*. Finally, the sea flow received by every cleft is not identical and this may be another factor influencing growth rate, as has been suggested by FISCHER-PIETTE (1939) for *Patella vulgata*.

Summer growth rate decrease coinciding with the beginning of the spawning season has been described for Littorinids (BORKOWSKI, 1974). The spawning season for *Fissurella crassa* has not been determined; there may be a spawning period when the summer growth rate decrease is observed.

SUMMARY

The growth of the commercially important keyhole limpet *Fissurella crassa* was studied along the intertidal rocky shore of Huayquique, Northern Chile. A total of 360 animals were marked, using numbered little tags or notches, and measured during 19 months. Only 88 individuals (24.4%) were recaptured enough times to be analyzed. Growth rate among individuals of similar initial size was highly variable. *Fissurella crassa* seems to have a seasonal growth pattern. Rapid growth was observed in spring; then mean growth rate diminished in late spring and early summer, followed by an accelerated growth that declined in autumn and was low in winter months. A relation between mean growth rates and age of this species is proposed. Accordingly, commercial sizes should correspond to animals from 2 to 4 years old. Maximum probable size for this species is about 83 mm of shell length. Factors that may influence growth are discussed.

ACKNOWLEDGMENTS

I wish to thank Professor Dr. Robert T. Paine for his interest in my research and helpful advice. I am grateful to Professor Nibaldo Bahamonde, to Dr. José Stuardo and to Professor Francisco Riveros-Zúñiga who made useful suggestions to the manuscript. I am specially indebted to my husband for his continuous encouragement.

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Abnormality of Shell Plates in Three Chitons from New England

BY

PAUL D. LANGER

(1 Plate)

INTRODUCTION

MORPHOLOGICAL VARIATION from the normal chiton shell plate number of eight has been reported by over forty authors. These reports were partially summarized by TAKI (1932), FISCHER-PIETTE & FRANC (1960), and BURGHARDT & BURGHARDT (1969).

The occurrence of morphological variation among three species of circumboreal chitons, *Tonicella rubra* (Linnaeus, 1767), *T. marmorea* (Fabricius, 1780), and *Ischnochiton albus* (Linnaeus, 1767), was studied in two separate populations in northeastern New England. This paper presents a brief description of the types encountered, their frequency of occurrence, subtidal distribution, and attempts to relate these factors to environmental severity.

MATERIALS AND METHODS

Samples were collected monthly for two years from subtidal rock substrates using SCUBA. At Deep Cove in Eastport, Maine, the substrate within the sampling quadrat was placed in fine mesh bags at each of ten stations from mean low water to 13.5 m. This procedure insured an unbiased sampling of all size groups.

Differences in substrate size and composition at Cape Neddick in York, Maine, necessitated a different sampling approach. Individual chitons were removed from rocks with forceps and placed in separate vials. All samples were preserved in 10% buffered formalin and later transferred to 70% alcohol.

RESULTS

Table 1 presents a summary of the types of morphological variation identified, their frequency, and geographic location. All of the variants had less than eight shell plates: 7½, 7, or 6. The most frequent type encountered for *Tonicella rubra* (Figures 1 & 2), *T. marmorea* (Figure 3), and

Table 1

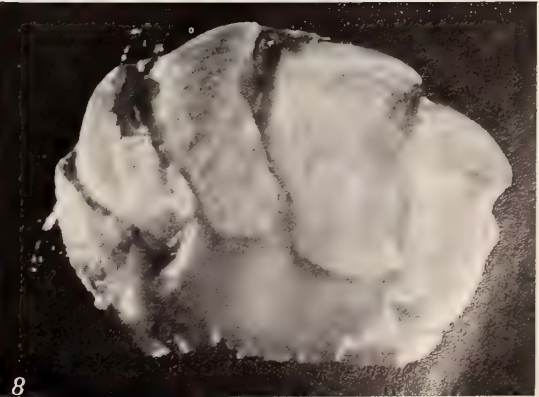
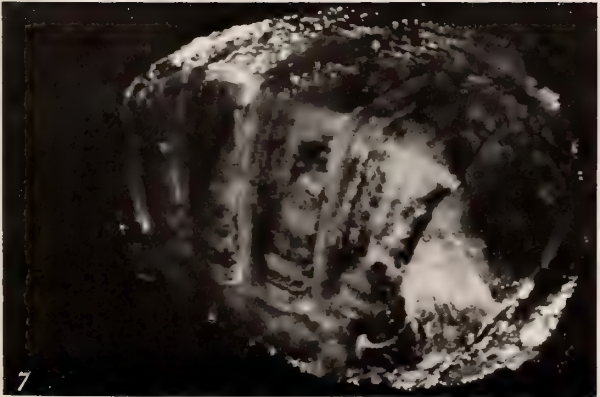
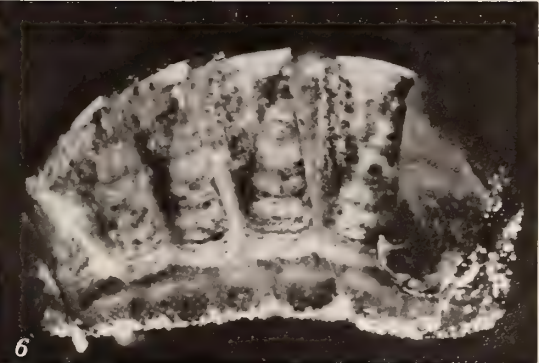
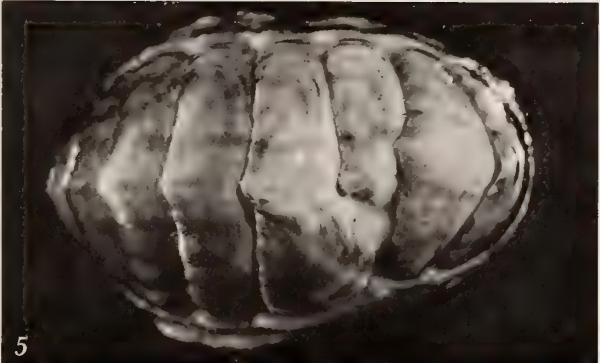
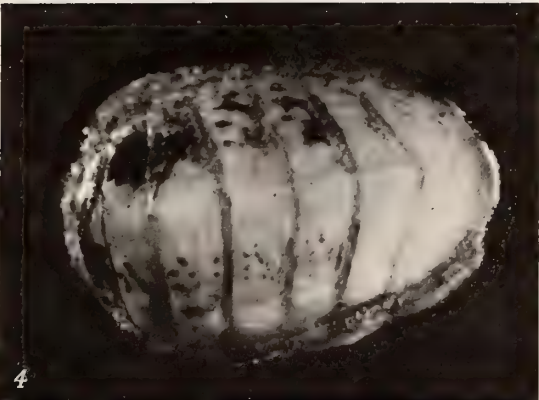
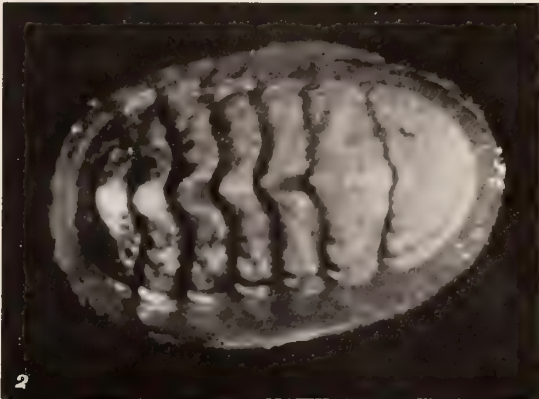
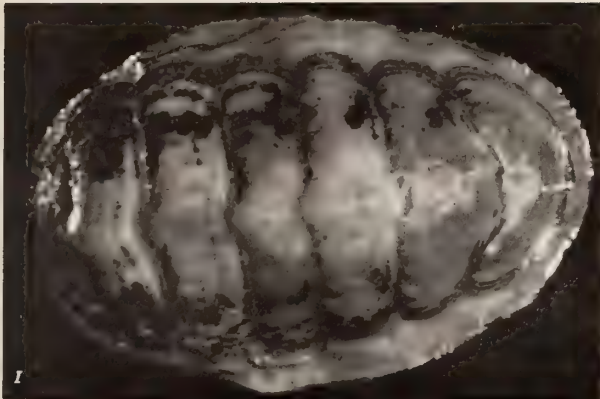
Frequency of Morphological Variation among Three Chiton Species.

Species	Shell Plate Number	Site	
		Deep Cove %	Cape Neddick %
<i>Tonicella rubra</i>		(2166) ¹	(1292) ¹
	7½	0.14	—
	7	0.46	0.54
<i>Tonicella marmorea</i>	6	0.046	—
		(1149) ¹	(487) ¹
	7½	—	—
<i>Ischnochiton albus</i>	7	0.35	0.21
	6	0.087	—
		(528) ¹	(—) ²
	7½	0.19	
	7	0.19	
	6	—	

¹Sample size²Absent from site

Explanation of Figures 1 to 8

Figure 1: *Tonicella rubra*, 7 shell plates; length, 11.7 mmFigure 2: *Tonicella rubra*, 7 shell plates; length, 8.4 mmFigure 3: *Tonicella marmorea*, 7 shell plates, length, 14.0 mmFigure 4: *Ischnochiton albus*, 7 shell plates; length, 9.9 mmFigure 5: *Tonicella rubra*, 7½ shell plates; length, 16.4 mmFigures 6 and 7: *Ischnochiton albus*, 7½ shell plates; length, 9.6 mm. Views showing highly modified 7th plateFigure 8: *Tonicella marmorea*, 6 shell plates; length, 8.1 mm



Ischnochiton albus (Figure 4) was the seven plated form. The 7½ plated variety, first described by OLIVER (1921), was found among *T. rubra* (Figure 5) and *I. albus* (Figures 6 & 7) populations, while the least common six plated form was represented only by the two *Tonicella* species (Figure 8). The frequency of all variant forms equaled or comprised less than one half of one percent of the total population. The diversity of variation was lower at the more exposed site, Cape Neddick.

Table 2

Frequency of Morphological Variation by Depth for Deep Cove.			
Depth (m)	<i>Tonicella rubra</i> %	<i>Tonicella marmorea</i> %	<i>Ischnochiton albus</i> %
MLW	0.00	0.00	0.00
1.5	0.87	0.00	0.00
3.0	0.46	1.30	0.00
4.5	0.84	0.00	1.70
6.0	0.55	1.10	0.79
7.5	1.26	0.45	0.00
9.0-13.5	0.00	0.00	0.00

Table 2 presents the benthic distribution of morphological variation. Data indicate there was no correlation between depth and variant frequency or depth and variant type. A correlation occurred between frequency of variation and the depth intervals of greatest population density.

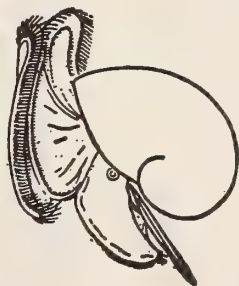
DISCUSSION

This is the first report of shell plate variation among *Tonicella marmorea* and *Ischnochiton albus*. According to TAKI (1932: 59). BLANEY (1904) reported a six plated *T. rubra*. However, no mention of this was found in BLANEY's (1904) original paper.

The benthic distribution of variants and their greater frequency at the environmentally less severe Deep Cove site suggest that occurrence of variants is not directly influenced by surf-related factors, temperature, or salinity extremes. The frequency of variation did correlate with population density. If the variants are genetic mutants, then it logically follows that they are most frequent at depths of greatest population concentration. However, if the survival of mutants was selected against by environmental extremes, this would reduce their appearance at the more severe site, Cape Neddick. It seems unlikely that shell plate aberration would physically impair the survival of subtidal chitons.

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Accumulation of ^{14}C -Labelled Algal Exudate by *Mytilus californianus* Conrad and *Mytilus edulis* Linnaeus, An Aspect of Interspecific Competition

BY

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(1 Plate; 3 Text figures)

INTRODUCTION

THE CALIFORNIA SEA MUSSEL, *Mytilus californianus*, forms extensive beds in surf-swept rocky habitats along the Pacific Coast of North America (RICKETTS & CALVIN, 1952). The smaller, more cosmopolitan bay mussel *Mytilus edulis* lives in the same geographical region but is not at home in crashing waves and inhabits more protected bays, inlets and backwaters (JOHNSON & SNOOK, 1927). Both bivalve species (Figure 1) have adaptive features appropriate to their environments. For example, *M. californianus* possesses a heavy shell and a robust byssus for withstanding heavy wave shock. *M. edulis*, on the other hand, has a more delicate shell and is more weakly attached to the substratum, but its ability to crawl and thus avoid being smothered by sediments contributes to its success in quiet waters (HARGER, 1968 and 1971). However, there are instances where the two mussel species overlap (BLAYLOCK, 1978), and this condition indicates that factors other than morphological and behavioural differences may favor niche separation between these two mytilids. In many sympatric animal species, competition for food is one of the most significant factors limiting their distribution (COX, HEALY & MOORE, 1973). Thus, in view of the occasional, and usually inexplicable, distributional overlap of *Mytilus californianus* with *M. edulis*, we have examined feeding in the two species to explain differences in niche.

The Mytilidae, like the majority of bivalved Mollusca, filter feed upon particulate material in suspension (MORTON, 1967). In addition, there is evidence which suggests that mussels are capable of accumulating dissolved organic carbon compounds present in seawater (STEPHENS & SCHINSKE, 1961; PEQUIGNAT, 1973; WRIGHT, 1976).

Brown macrophytes release photosynthetically fixed dissolved and particulate carbon as a physiological function of normal growth (SIEBURTH & JENSEN, 1968; BRYLINSKY, 1977). Amounts of organic carbon released by these algae comprised a relatively small portion (usually <1%) of the carbon fixed (BRYLINSKY, 1977; FANKBONER & DE BURGH, 1977), but significantly, this material is accumulated by marine invertebrates *in situ* (FANKBONER, 1976; FANKBONER & DRUEHL, 1976) and thus may be assumed to be a normal component of their diets.

In this study, we have placed specimens of *Mytilus californianus* and *M. edulis* in direct competition for ^{14}C -labelled dissolved organic carbon (DOC) and particulate organic carbon (POC) exudated by a cohabiting kelp *Macrocystis integrifolia* Bory. We have used algal exudated material rather than specific synthetic substrates because it may more accurately represent food material available *in situ* to *M. californianus* and *M. edulis*.

MATERIALS AND METHODS

Preparation of ^{14}C -labelled organic carbon compounds:

A single blade from the frond of *Macrocystis integrifolia* was enclosed with 2.0 L of ambient seawater plus 1.0 mC of $\text{NaH}^{14}\text{CO}_3$ (Atomic Energy of Canada) in a clear polyethylene 6.5 x 17.5 x 38 cm bag. This provided a ^{14}C source for photosynthesis leading to production of materials exudated as isotope labelled dissolved organic carbon and particulate organic carbon. Blades were selected from *M. integrifolia* which were obviously healthy, advanced in growth (50-70 cm in length) but immature. If mature or late growth blades are used for producing algal exudation

materials, one runs the risk of obtaining the products of microbial decomposition of plant tissue rather than algal exudate *per se* (FANKBONER & DE BURGH, 1977).

The kelp blade was incubated for 24 h in the ^{14}C -labelled bag waters. At the end of the incubation period, the incubation waters were removed and processed as follows for feeding ^{14}C -labelled particulate and dissolved organic carbon compounds to *Mytilus*.

Particulate organic carbon (POC): Incubation waters from the blade of *Macrocystis integrifolia* consist of three categories of ^{14}C -labelled components; these include dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and particulate organic carbon (POC). HAMMON & OSBORNE (1959) have demonstrated that representatives from 12 major invertebrate phyla are capable of fixing DIC into acids of the Krebs' citric acid cycle. The significance of carbon fixation of these organisms remains to be assessed, but to prevent loss of precision in our DOC accumulation determinations, we removed DIC from the incubation waters by acidification prior to separation of DOC from POC. Kelp blade incubation waters were acidified with concentrated HCl to pH 2.5 and left standing in a fume hood for several hours to evolve $^{14}\text{CO}_2$. Next, the pH of the incubation waters was readjusted to pH 7.9 by addition of solid pellets of NaOH; 500 mL of the incubation waters were used, as is, to provide a ^{14}C -labelled particulate organic carbon fraction for feeding to the mussels. Because this medium contains both labelled DOC and POC, ^{14}C -activity of POC may be estimated by the subtraction method using activity data taken from isolated ^{14}C -labelled DOC below.

Dissolved organic carbon (DOC): The second 500 mL volume of the ^{14}C -DIC free kelp incubation waters was filtered through 0.22 μm Millipore membranes to separate ^{14}C -labelled DOC from the particulate portion of the waters.

Composition of kelp exudated DOC and POC: Translocation studies on brown macrophytes (NICHOLSON & BRIGGS, 1972; SCHMITZ & SRIVASTAVA, 1974a & 1974b) indicate that the DOC fraction of kelp exudation material is a 1:1 mixture of D-mannitol and amino acids. However, the particulate component of kelp exudate or algal humic material (SIEBURTH & JENSEN, 1968; SIEBURTH, 1969) is less well understood. It is not within the scope of this study to delve into the biochemistry of kelp exudated POC; however, we have described the gross morphological features characterizing exudation particulates via scanning electron microscopy.

To view the physical structure of particulate material fed to our experimental animals, a 1.0 mL sample of algal exudate was filtered through a 0.22 μm Millipore membrane. Next, the particulate coated filter was fixed for one hour in a solution of 4% glutaraldehyde buffered in 0.2 M cacodylate at pH 7.4. The 4% glutaraldehyde solution was formulated from a 25% prebuffered (3% calcium carbonate) stock solution of "Fisher" biological grade glutaraldehyde. Following a brief rinse in distilled water, the particulate matter was post-fixed for 24 hours in 2% osmium tetroxide buffered with Dorey's Solution B (DOREY, 1965). Following a brief rinse in distilled water, the fixed material was dehydrated by first quenching it in liquid nitrogen, and then freeze drying under vacuum. The dried POC (still upon the membrane filter) was mounted on a stub, gold coated, viewed and photographed using an ETEC Autoscanning electron microscope.

Feeding experiments: Specimens of *Mytilus californianus* and *M. edulis* (Figure 1) were collected intertidally from a single mixed bed in the Ross Islets, Barkley Sound, Vancouver Island, British Columbia. The mussels were approximately equal in size and possessed a mean length of 1.5 cm.

To condition the mussels to their feeding aquaria, twenty individuals of each species were placed in two aquaria containing 3.0 L of 0.22 μm Millipore filtered seawater. The aquaria were maintained at a temperature of 12°C and constantly aerated to insure oxygenation and circulation of the medium. The mussels were considered acclimatized to the aquaria when they had laid down several byssal anchoring threads; byssal attachment by *Mytilus* was generally completed within 24 hours.

At the onset of the feeding experiments, 500 mL of ^{14}C -labelled algal exudate were added to each aquarium with one aquarium containing exudate including both dissolved and particulate organic carbon and the other consisting of 0.22 μm Millipore filtered exudate dissolved organic carbon only. Five heat killed control animals of each species were then added to each aquarium. At intervals of 0.5, 1.5, 3.0, 5.0 and 7.0 hours, 4 live specimens and 1 killed control specimen of each mussel species were removed from both aquaria. The gills, mantle and visceral mass were immediately dissected from each mussel and separately dried, weighed and burned in a combustor (Searle Analytic Corp.). The $^{14}\text{CO}_2$ evolved was captured in a 2:3 cocktail of Oxisorb- CO_2 :Oxiprep-1 (New England Nuclear) and counted for ^{14}C -activity. To monitor the ^{14}C -activity present in the experimental feeding aquaria, a 2.0 mL sample was collected from each aquarium at the

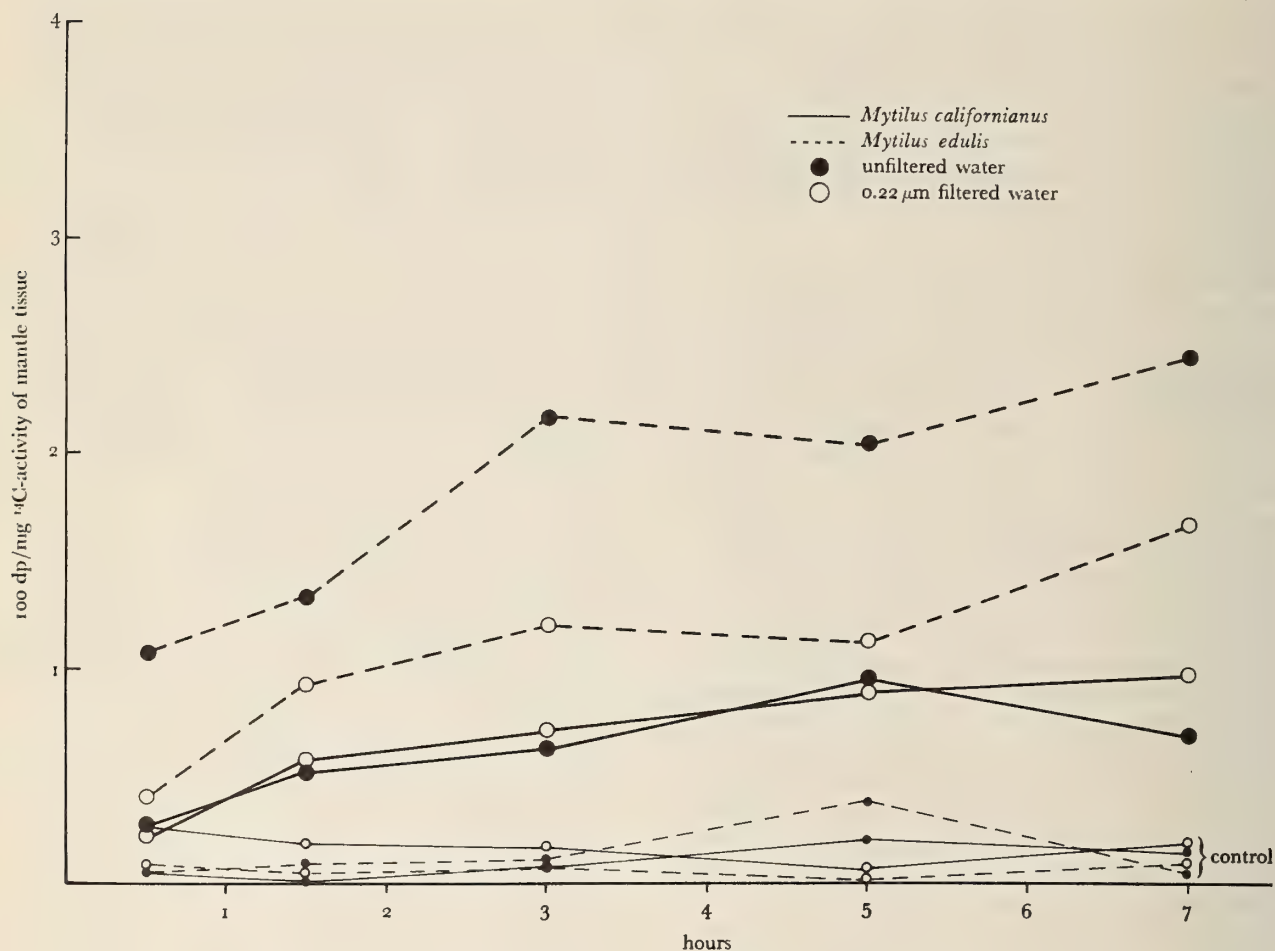


Figure 3

Rates of accumulation of ^{14}C -labelled algal exudation material by the mantle tissues of *Mytilus californianus* and *M. edulis*. *Nota bene*: in this figure and those to follow, $0.22\ \mu\text{m}$ filtered waters contain ^{14}C -DOC while the unfiltered waters include both ^{14}C -DOC and ^{14}C -POC.

Explanation of Figures 1 and 2

Figure 1: The "sea mussel" *Mytilus californianus* Conrad (left) is distinguished by its thicker shell with 12 radial grooves from the lighter, smooth-valved "bay mussel" *Mytilus edulis* Linnaeus (right)
 Figure 2: A scanning electron photomicrograph of the particulate fraction of exudation material released by the "large kelp" *Macrocystis integrifolia* Bory. The particulate, light-toned substance is principally algal humic material which has been sloughed from the blade surfaces of the kelp.

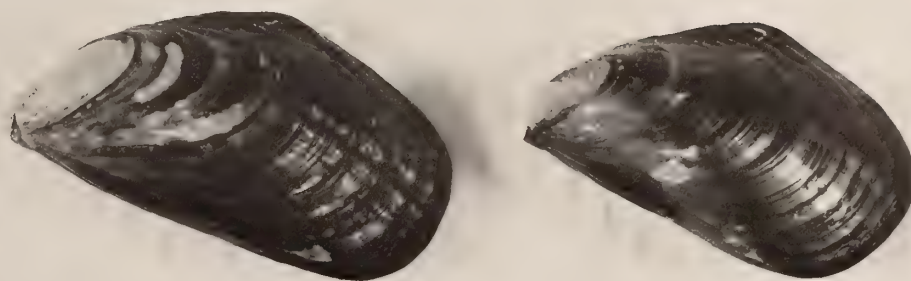


Figure 1

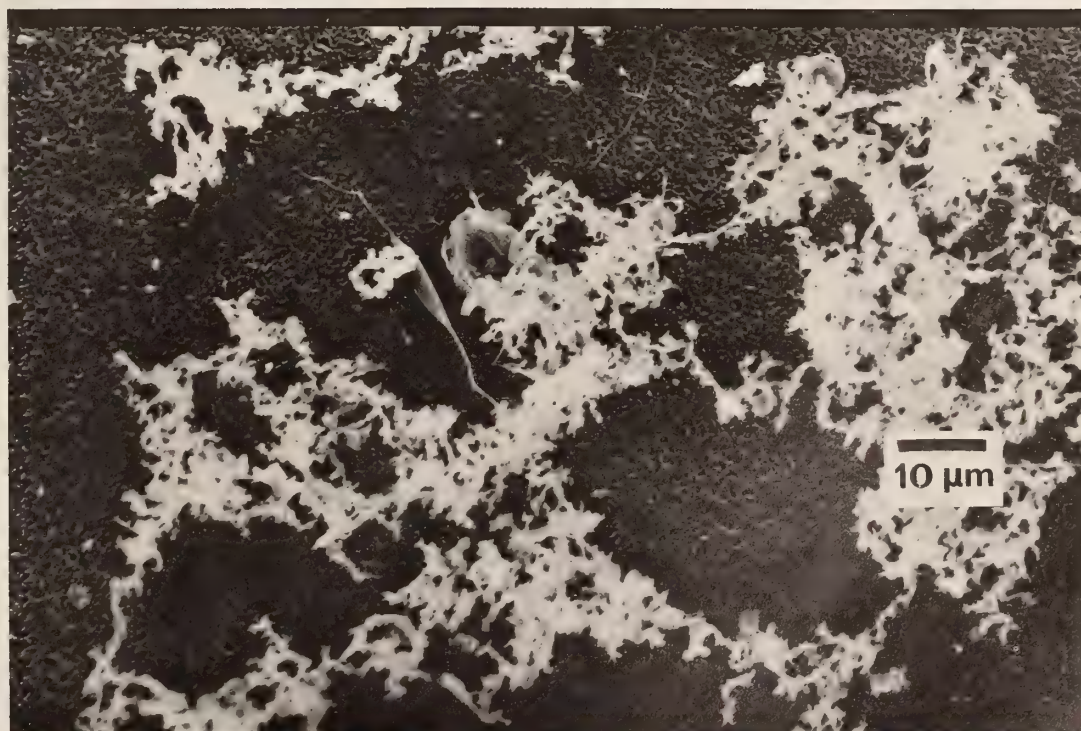


Figure 2



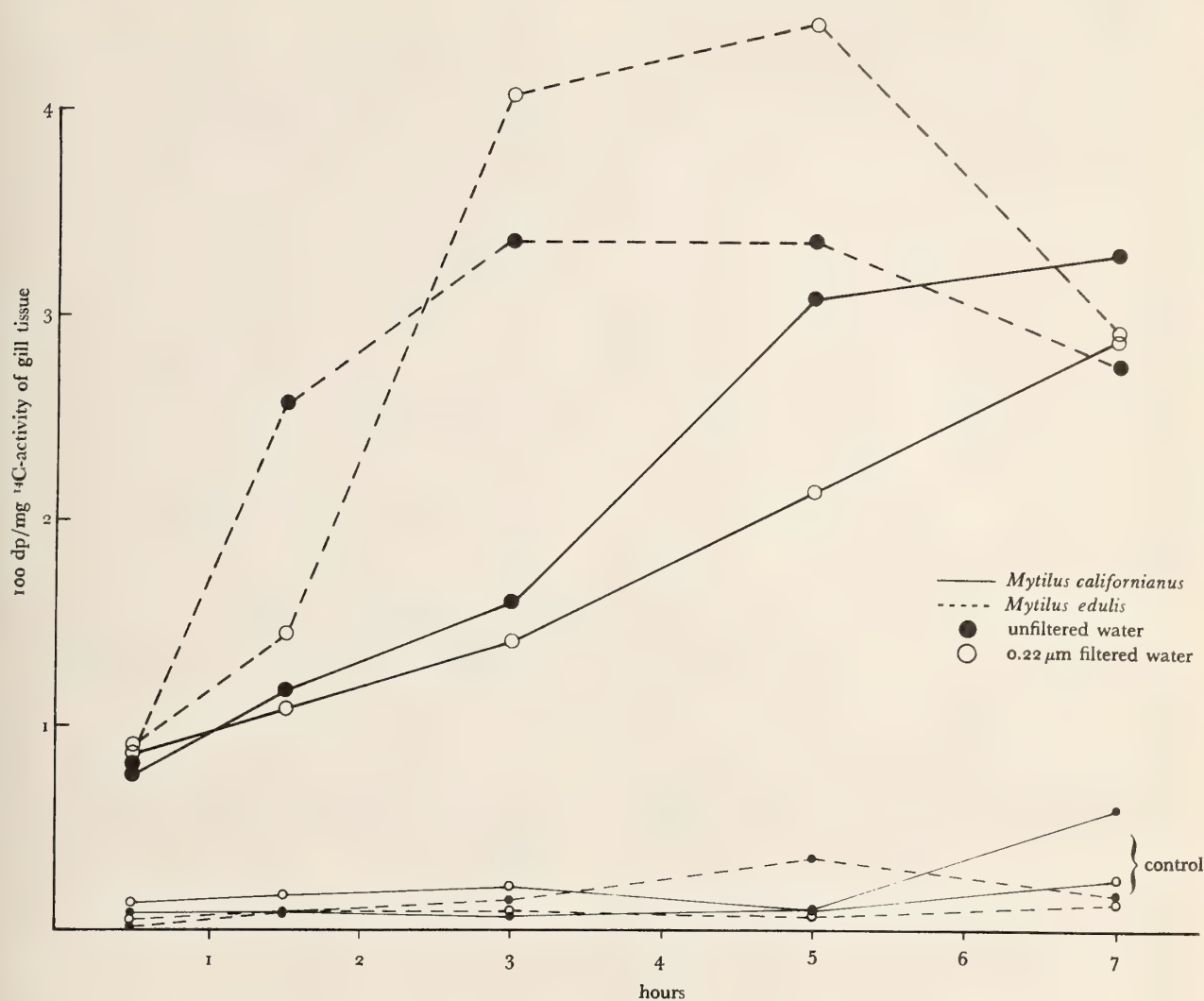


Figure 4

Rates of accumulation of ^{14}C -labelled algal exudation material by the gill tissues of *Mytilus californianus* and *M. edulis*

five sampling periods described above and filtered through a Millipore $0.22\ \mu\text{m}$ filter. The dissolved fraction passing through the filter was added to 10 mL of 'Aquasol' (New England Nuclear) and counted for ^{14}C -activity. The particulate fraction of the sample retained by the membrane filter was combusted, collected, and counted as above. All counts were corrected for background quenching by the external standard method, and were converted to disintegrations per minute (DPM). Graph data points (Figures

3, 4 & 5) represent mean values (significant at the 0.5 level) of ^{14}C -activity per unit dry tissue weights.

RESULTS

Algal exudate: Throughout the seven hour experimental feeding period, ^{14}C -activity levels of DOC in both aquaria remained constant at approximately 10,000 DPM/mL.

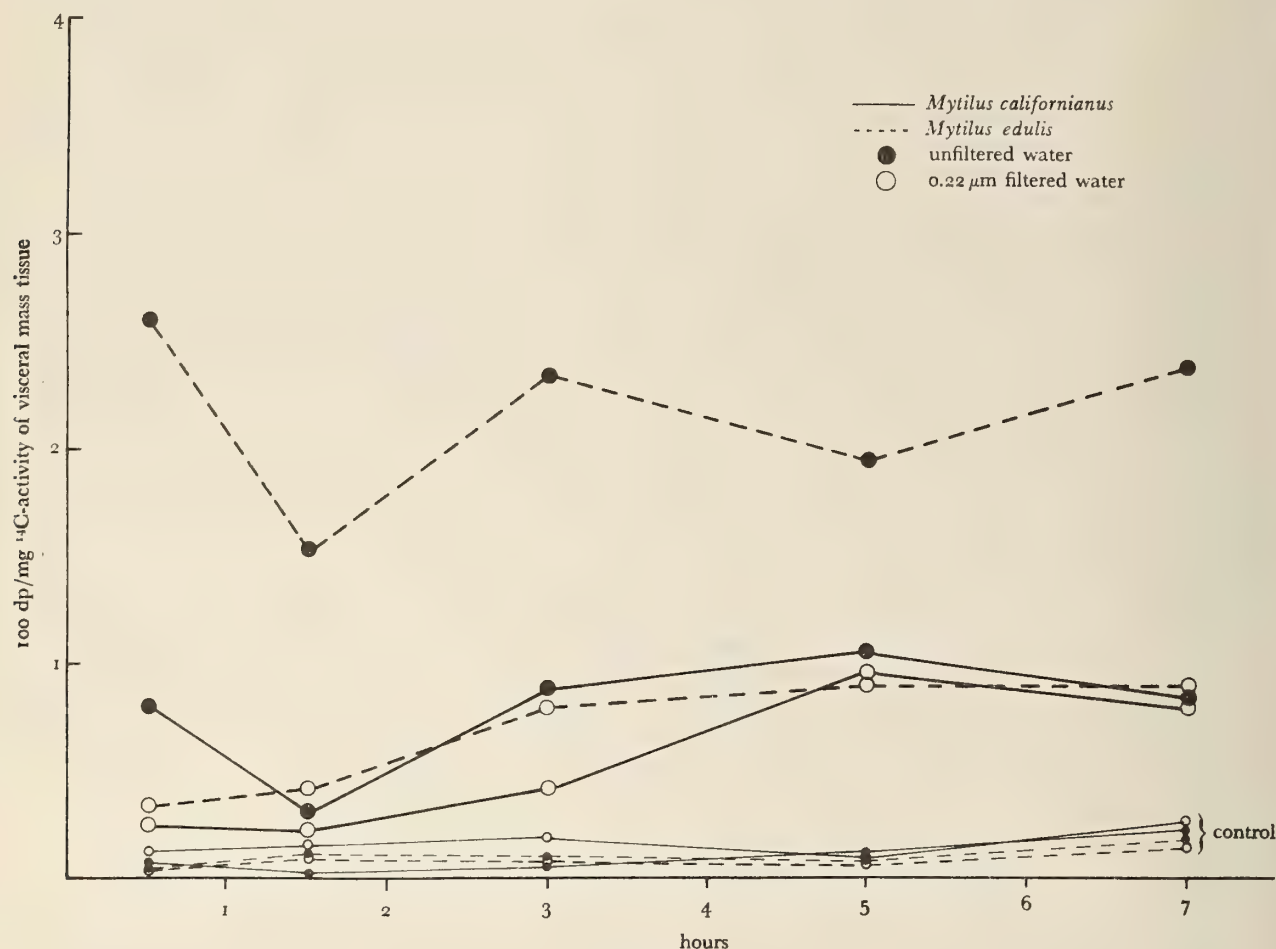


Figure 5

Rates of accumulation of ^{14}C -labelled algal exudation material by the visceral mass tissues of *Mytilus californianus* and *M. edulis*

Particulates collected on Millipore filters also exhibited a uniform level of activity, equivalent to 50 DPM/mL. The ratio of dissolved to particulate ^{14}C -activity was therefore in the order of $2 \times 10^2 : 1$, the same order of magnitude as DOC/POC present in natural waters (SHARP, 1973). Scanning electron photomicrographs of particulate carbon fed to *Mytilus* revealed that the dominant component in POC was fibrous plant material (Figure 2) sloughed from blade surfaces of *Macrocystis integrifolia* during incubation. In addition, the POC included small amounts of diatomaceous material (*Skeletonema* and *Coscinodiscus*), plus naked dinoflagellates (unidentified). Algal exudation material appeared to contain relatively few bacteria; this observation concurs with the results of pre-

vious studies (BRYLINSKY, 1977; FANKBONER & DE BURGH, 1977) on exudation by brown macrophytes.

Accumulation of ^{14}C -activity by *Mytilus*: The data presented in Figure 3 indicate that mantle tissues in *Mytilus edulis* accumulate nearly twice the ^{14}C -activity in unfiltered water (DOC & POC) as in filtered water (DOC). Overall, mantle tissues in *M. edulis* clearly accumulate higher levels of DOC than did *M. californianus* in either filtered or unfiltered algal exudate.

Accumulation of ^{14}C -labelled kelp exudation material by the gills of *Mytilus edulis* was significantly higher than in the case of *M. californianus* throughout the first five hours of the feeding period (Figure 4). However, a com-

parison of the mean values of ^{14}C -activity levels in the gills following seven hours revealed a sudden increase in levels of accumulation of DOC resulting in no significant differences in gill tissue activities between the two mussel species. Deceleration in rate of DOC accumulation by the gills of *M. edulis* is consistent with observed activity during digestive cycles (LANGTON, 1977) and normal periods of rhythmicity in rates of filtration currents (RAO, 1954; JØRGENSEN, 1955). Specimens of *M. californianus*, on the other hand, are not influenced by a rhythm or periodicity in their feeding rates (SEGAL, RAO & JAMES, 1953), and throughout the experiments have uniformly increased ^{14}C -activity levels in both mantle and gill tissues.

In aquaria containing filtered exudation waters (DOC), accumulation of DOC by visceral mass tissues from both mussel species increased steadily throughout the seven hours of the experiment (Figure 5) without any significant differences developing between the two species. However, in aquaria containing unfiltered medium (DOC & POC), *Mytilus edulis* concentrated ^{14}C -activity in the visceral mass to levels approximately one order of magnitude greater than did *M. californianus* (Figure 5). These results indicate that there exists a difference in particulate feeding efficiency between the two mytilid species. Therefore, dry weights of gills and viscera from each species were averaged and compared yielding ratios of gill weights to viscera weights of 0.488 for *M. edulis* and 0.349 for *M. californianus* (significant at the 0.5 level). Thus it is apparent that in comparison to *M. californianus*, *M. edulis* possesses a larger gill in relation to its size. This morphological difference permits *M. edulis* to filter feed on algal exudate at a higher rate than *M. californianus* with a consequential increase in the relative ^{14}C -activity of its visceral mass.

DISCUSSION

The data demonstrate that both *Mytilus californianus* and *M. edulis* accumulate dissolved and particulate organic carbon exudated by the "large kelp" *Macrocystis integrifolia*. In our measurements of DOC taken up by mussels, we found that on a ^{14}C -activity to tissue weight basis, *M. edulis* was generally superior to *M. californianus* in its ability to accumulate DOC. However, in the case of POC, *M. edulis* accumulated approximately one order of magnitude more activity over the same feeding period than did *M. californianus*. We have concluded that the possession of a larger gill in *M. edulis* contributes to higher feeding rates and earlier physiological studies on mussel feeding support this contention. For example, JØRGENSEN (1955) has shown that filtration rates in juvenile specimens of *M. edulis* may be 18 to 30 times greater than for *M. californianus*.

Moreover, the degree of tidal exposure may also affect filtration rates in mussels. Although *M. californianus* appears to be unaffected by its vertical position in the intertidal (SEGAL, RAO & JAMES, 1953), with *M. edulis*, filtration activity may increase or decrease as a function of intertidal height (JØRGENSEN, 1960). Thus, in addition to significantly superior filtration rates by *M. edulis* over its vertical range as its position becomes higher in the intertidal range, so does its rate of filtration.

Interspecific differences in the gill size between *Mytilus californianus* and *M. edulis* not only affect competition for food, but in addition, may directly influence their survival in sediment rich waters. *A priori*, given the same size of mussel, a larger gill would be capable of handling greater amounts of sediment than a smaller one. Therefore, climbing ability by *M. edulis* (HARGER, 1971) may be only one of several factors influencing smothering by sediment material.

In summarizing his investigations of competition between *Mytilus edulis* and *M. californianus*, HARGER (1971) has stated that all traits which he considers to be important in competitive interactions between the two mussel species appear to be adaptations to the physical environment. These traits include the heavier shell and greater byssal thread production in *M. californianus* and the crawling behaviour in juvenile specimens of *M. edulis*. However, we have concluded that in addition, greater gill size in *M. edulis* resulting in a superior ability to accumulate dissolved and particulate organic carbon gives this mussel a significant nutritional advantage over the more physically robust *M. californianus*. Further, we suggest that in protected sediment-laden waters, a larger gill in *M. edulis* may favor its survival over *M. californianus*. We believe that niche separation in *Mytilus* should not be interpreted solely upon the basis of mechanical adaptations to physical stress but should include, as well, aspects of the mussels' physiology.

Despite the fact that dissolved and particulate organic carbon is taken up and utilized by a variety of marine invertebrates, the over all significance of this food source is not fully understood (see reviews by STEPHENS, 1967, 1968, & 1972; RILEY, 1970; WEST, DE BURGH & JEAL, 1977). Nearly all previous study on uptake of DOC has evolved around the rate of accumulation of a synthetic substrate(s) by a single species or its tissues. This approach is a sound one because it permits greater control over experimental conditions, but has the disadvantages that food materials for accumulation are not generally available to the organism in a natural form and under conditions to which the organism would normally be exposed. In this report, we take the position that to determine significance of DOC and POC as a food source for marine organisms, one ap-

proach is to use accumulation of naturally occurring organic carbon as a tool to examine specific and existing ecological questions. In doing so, we have shown significant interspecific differences in *Mytilus californianus* and *M. edulis* which contribute to niche separation.

ACKNOWLEDGMENTS

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Studies on the *Mytilus edulis* Community in Alamitos Bay, California: VII. The Influence of Water-Soluble Petroleum Hydrocarbons on Byssal Thread Formation

BY

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INTRODUCTION

Mytilus edulis, Linnaeus, 1758, is the predominant organism associated with docks, pilings, and boat floats in Alamitos Bay (REISH, 1964a). Occasionally red tide blooms decimate the *M. edulis* population as well as the diverse assemblage of polychaetes, amphipods, and other fauna which comprise the *M. edulis* community (REISH, 1964a, 1964b). It is not known whether the mussels were affected directly by an accumulation of a toxic substance secreted by the dinoflagellates or indirectly by the decrease of dissolved oxygen in the water due to bacterial decomposition of organic material. A drastic reduction in byssal thread production was observed under laboratory conditions for *M. edulis* exposed to dissolved oxygen concentrations below 0.9 ppm (REISH & AYERS, 1968), which is higher than the 0.1 ppm observed in Alamitos Bay during the 1962 red tide.

It seems logical to assume that byssal thread production is a reasonable parameter with which to gauge the metabolic activity or physiological functioning of *Mytilus edulis*. The ability of *M. edulis* to form byssus attachments is crucial to the survival of this organism. MARTIN *et al.*, (1975) have shown that byssal thread production may be used as an indicator of the dose response to heavy metal toxicants.

Due to the activity of motor powered vessels within the Alamitos Bay area, petroleum hydrocarbons are a pollutant with which the *Mytilus edulis* community must contend. The purpose of this present investigation was to

determine what effect the water-soluble fraction of three different oils had on the capacity of *M. edulis* to form byssal threads in the laboratory.

MATERIALS AND METHOD

Mytilus edulis specimens were collected from boat docks in Alamitos Bay during the month of July. Only mussels from 18 to 23 mm in width were used. Limiting specimens to this size range insured that no gravid individuals would be included. GLAUS (1968) showed that small *M. edulis* produce more byssal threads than do larger ones under optimum conditions. Several hundred mussels of the appropriate size were acclimated at $19.5 \pm 0.5^{\circ}\text{C}$ for three days. Prior to the start of the experiment, the valves were scraped clean of fouling organisms and all byssal threads were cut.

Two of the oils used in this study were South Louisiana crude oil and No. 2 fuel oil which were originally supplied by the American Petroleum Institute and redistributed by Dr. Jack W. Anderson of Texas A&M University. A commercially available oil, Sta-lube 50:1 2 cycle outboard motor oil was also tested. The procedure for preparation of the water-soluble fraction (WSF) of the oils was similar to the method employed by ANDERSON *et al.*, (1974a). Nine parts millipore filtered ($0.45\ \mu\text{m}$) seawater was stirred with one part oil on a magnetic stirrer for 20 hours at a slow speed. After stirring, the aqueous phase was siphoned off and utilized immediately in experiments. A detailed liquid-gas chromatographic analysis of the two API reference oils and their WSFs was carried out earlier by Dr. J. Scott

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Warner, Battelle Memorial Laboratories (ANDERSON *et al.*, 1974).

All experiments were conducted at $19.5 \pm 0.5^\circ \text{C}$ with millipore filtered ($0.45 \mu\text{m}$) seawater. The bioassay containers employed were 500 mL Erlenmeyer flasks. Each flask contained 100 mL of the appropriate test solution with one mussel per flask. Concentrations of 25, 50, 75, and 100% of the initial WSF were tested for each of the three oils. The solutions were not changed or replenished during the course of the experiment. No food was administered throughout the duration of the experiment. Byssal thread production and survival were observed at 1, 2, 3, 4, 7, and 14 days. Because the data did not conform to analysis by parametric techniques, the non-parametric ranking test of Mann and Whitney was utilized to determine significant differences in byssal thread production.

RESULTS

The influence of the WSFs of South Louisiana crude oil, No. 2 fuel oil and Sta-lube outboard motor oil are presented in Tables 1, 2, and 3, respectively. Byssal thread production was significantly inhibited at the 100% WSF for all three oils. For South Louisiana crude oil and No. 2 fuel oil this inhibitory influence was significant throughout the duration of the experiment. For the Sta-lube outboard motor oil the inhibition of byssal thread production was only significant up until the 72 hour check. South Louisiana crude oil was most effective in its inhibitory influence on a percent WSF basis while the Sta-lube outboard motor oil produced the least effect.

An unexpected result of this experiment was that a significant enhancement in byssal thread production was observed for all three WSFs at concentrations below those at which an inhibitory effect was elicited. At 96 hours a significant enhancement was observed at 25% of the WSF for South Louisiana crude and No. 2 fuel oil while 50% of the WSF of Sta-lube outboard motor oil produced a similar stimulation as compared with the control. In a repeat experiment, 25% WSF of No. 2 fuel oil produced a fourfold increase in byssal thread production as compared with the control after 96 hours of exposure. This stimulation of byssal thread formation, however, was not significant beyond 96 hours for any of the three WSFs.

DISCUSSION

The WSF of South Louisiana crude oil and No. 2 fuel oil have been analyzed by UV and IR spectrophotometry and

were shown to contain 19.8 mg/L and 8.7 mg/L total hydrocarbons, respectively (ANDERSON *et al.*, 1974a). Of the hydrocarbons in the No. 2 fuel oil WSF, approximately 39% are aromatic compounds as compared to less than 2% aromatics for the WSF of South Louisiana crude oil. The soluble aromatic and naphthalene compounds of an oil produce the majority of its toxic effect (ANDERSON *et al.*, 1974b). These compounds are highly volatile, however, as the naphthalene compounds have been observed to reach undetectable levels under similar bioassay conditions after 96 hours (CARR & REISH, 1977). The higher molecular weight ($> \text{C}_{10}$) water-soluble paraffinic hydrocarbons are not nearly as volatile as the aromatic ones (DODD, 1974), and hence their relative percentage of the total hydrocarbons present in solution increases with time.

An examination of Tables 1 and 2 indicates that South Louisiana crude oil was the most effective inhibitor of byssal thread production on a percent WSF basis. Since the WSF of South Louisiana crude oil contains the highest concentration of paraffinic hydrocarbons, which are the least volatile of the water-soluble hydrocarbons, it appears likely that these higher molecular weight ($> \text{C}_{10}$) aliphatic compounds are at least partially responsible for the chronic inhibition of byssal thread formation. In the two refined oils, whose WSFs contain a higher percentage of volatile aromatics, the suppression of byssal thread formation was not nearly as marked.

Other studies have shown the WSF of No. 2 fuel oil to be more toxic than South Louisiana crude oil on a percent WSF and total initial hydrocarbon basis for a variety of marine organisms (ANDERSON *et al.*, 1974; ROSSI *et al.*, 1976; CARR & REISH, 1977). In the present study at 14 days the 100% WSF crude oil group suffered 40% mortality whereas in the 100% WSF of the No. 2 fuel oil only 20% mortality was observed. These were the only deaths occurring during the course of the experiment. While this difference in survival rates is not statistically significant, the relative mortality rate follows the trend seen in suppression of byssal thread production. Again, the most deleterious effects were produced by the WSF of South Louisiana crude oil. It appears that unlike most of the other marine organisms which have been tested that *Mytilus edulis* is more susceptible to contamination by crude oil than by these refined oils.

The unanticipated result of a statistically significant stimulation by byssal thread production was observed for all three WSFs up until 96 hours after which time the stimulatory effect although evident was not significant statistically. When considering the changes in hydrocarbon composition occurring in the WSF over a 96 hour time

Table 1

Influence of Seawater-Soluble Fraction (WSF) of South Louisiana Crude Oil on Byssal Thread Production of *Mytilus edulis*. Tests for Statistical Observations and Significance.

Experimental Concentrations as Percent WSF	24 hours		48 hours		72 hours		96 hours		7 days		14 days	
	Average No. of Byssal Threads	U ¹	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U
Control n = 20	5.75	—	9.85	—	12.6	—	15.55	—	28.4	—	39.15	—
25 n = 10	8.2	123.5	17.3	150 ²	18.6	133	24.6	146.5 ²	42.3	130	58.6	131.5
50 n = 10	2.5	137	5.1	126.5	5.7	146 ³	8.2	133.5	12.0	131.5	21.4	125.5
75 n = 10	1.1	159.5 ³	3.2	151.5 ³	3.4	1.54 ³	3.9	171 ³	7.5	163.5 ³	15.2	150.5 ³
100 n = 0	0	185 ³	0.1	193 ³	0.1	193 ³	0.1	199 ³	1.4	191 ³	4.1	177.5 ³

¹Mann-Whitney U statistic comparing experimental populations with the control. U statistic at .05% level of significance = 138.

²Significant increase in byssal thread production.

³Significant decrease in byssal thread production.

Table 2

Influence of Seawater-Soluble Fraction (WSF) of No. 2 Fuel Oil on Byssal Thread Production of *Mytilus edulis*. Tests for Statistical Observations and Significance.

Experimental Concentrations as Percent WSF	24 hours		48 hours		72 hours		96 hours		7 days		14 days	
	Average No. of Byssal Threads	U ⁴	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U
Control n = 20	5.75	—	9.85	—	12.6	—	15.55	—	28.4	—	39.15	—
25 n = 10	13.3	132.5	24.8	146.5 ⁵	29.4	144 ⁵	43.2	144 ⁵	47.2	133.5	57.3	134
50 n = 10	3.3	131.5	9.0	102	13.4	106.5	18.5	123.5	31.3	108	37.2	120
75 n = 10	0.3	178.5 ⁶	8.8	106.5	11.4	102.5	15.8	102.5	25.3	100.5	39.1	101.5
100	0	185 ⁶	0.1	197 ⁶	0.2	190.5 ⁶	2.8	178 ⁶	6.8	161.5 ⁶	16.1	148 ⁶

⁴Mann-Whitney U statistic comparing experimental populations with the control. U statistic at .05% level of significance = 138.

⁵Significant increase in byssal thread production.

⁶Significant decrease in byssal thread production.

period, the evaporation of the volatile aromatics and naphthalenic compounds, particularly, is the most predominate change. The stimulation of byssal thread formation decreases at approximately the same time that the naphthalenic compounds reach undetectable levels in the WSF, lending credence to the possibility that these aromatic and polyaromatic compounds may be responsible for this observed stimulatory effect. Additional tests with specific aromatic and naphthalenic compounds would further elucidate this hypothesis. Most likely there is no specific hydrocarbon that is causing this effect but rather a combination of compounds which is responsible.

This is not the first time that exposure to low-level water-soluble hydrocarbons has produced a stimulation of some physiological process in marine organisms. NEFF *et al.*, (1976) observed an increased growth rate with zoea of the mud crab *Rhithropanopeus harrisi* exposed to sublethal concentrations of No. 2 fuel oil. TATEM (1975) observed an increase in the number of larvae produced in the grass shrimp *Palaemonetes pugio* when exposed to sublethal WSFs of No. 2 fuel oil. Rossi (1976), conducting an investigation through several generations with the poly-

chaete *Neanthes arenaceodentata*, observed a decrease in oocyte maturation as compared with the control for all exposure concentrations. Reproduction was significantly stimulated in the polychaete *Ophryotrocha diadema* exposed to an initial total hydrocarbon concentration of 1.99 ppm of South Louisiana crude oil (CARR & REISH, 1977). Similar phenomena have been observed in toxicity tests with rats and mice (SMYTH, 1967). Smyth suggests that the increased growth and reduced mortality observed in toxicity tests with low levels of known noxious substances is due to the exercising of homeostatic mechanisms. It seems likely that a similar phenomenon is occurring in some marine animals exposed to water-soluble hydrocarbons.

When considering the results of these experiments and how they relate to the natural environment, it is worthy of noting that the type of water-soluble hydrocarbons most commonly entering the harbor waters (outboard motor fuel) produces the least inhibition of byssal thread production. Since *M. edulis* characteristically inhabits floating boat docks near the air-water interface, these mussels would be exposed to a greater threat than that posed by water-soluble hydrocarbons were a large oil spill to take place

Table 3

Influence of Seawater-Soluble Fraction (WSF) of Sta-lube Outboard Motor Oil on Byssal Thread Production of *Mytilus edulis*. Tests for Statistical Observations and Significance.

Experimental Concentrations as Percent WSF	24 hours		48 hours		72 hours		96 hours		7 days		14 days	
	Average No. of Byssal Threads	U ⁷	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U	Average No. of Byssal Threads	U
Control n = 20	5.75	—	9.85	—	12.6	—	15.55	—	28.4	—	39.15	—
25 n = 10	10.0	132	14.8	122.5	16.6	120.5	20.8	116.5	26.5	104	28.8	106
50 n = 10	16.3	142 ⁸	21.4	140 ⁸	25.9	142 ⁸	31.8	138 ⁸	39.1	125	48.8	118.5
75 n = 10	2.8	123	8.7	113	11.6	115	18.1	101.5	23.2	104.5	28.1	113
100	1.0	171 ⁹	4.2	153 ⁹	4.5	154 ⁹	10.2	135	22.2	104	27.4	109.5

⁷Mann-Whitney U statistic comparing experimental populations with the control. U statistic at .05% level of significance = 138.

⁸Significant increase in byssal thread production.

⁹Significant decrease in byssal thread production.

locally. Their proximity to the air-water interface would allow floating oil to strand on these mussels causing physical smothering under extreme conditions. Although not as dramatic, chronic exposure to sublethal water-soluble hydrocarbons might also lead to the decline or eradication of a population in a less conspicuous manner.

The results of this study suggest that the levels of water-soluble hydrocarbons currently found in Long Beach Harbor due to motor boat activity pose little threat to the survival of *Mytilus edulis*. The levels of water-soluble hydrocarbons necessary to cause deleterious effects would only be found associated with a local spillage of oil. Certain areas receiving chronic low level hydrocarbon insult may not be suitable for survival of *M. edulis*. Barring the event of any local oil spills, *M. edulis* population levels are more dependent on the periodic red tide phenomenon than the effects resulting from local motor boat usage. Why low water-soluble hydrocarbon levels produce stimulation of byssal thread production is a question which awaits further investigation.

SUMMARY

1. The bay mussel *Mytilus edulis* was exposed to varying concentrations of the water-soluble fraction (WSF) of No. 2 fuel oil, South Louisiana crude oil and Sta-lube outboard motor oil and the number of byssal threads produced was recorded at intervals over a 14 day period.
2. Byssal thread production was significantly inhibited at the 100% WSF for all three oils.
3. South Louisiana crude oil was the most effective in its inhibitory influence on a percent WSF basis while the Sta-lube outboard motor oil produced the least effect.
4. An unexpected result of this experiment was that a significant enhancement in byssal thread formation was observed for all three WSFs at concentrations below those at which an inhibitory effect was elicited.

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Distributional Patterns of Juvenile *Mytilus edulis* and *Mytilus californianus*

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INTRODUCTION

Mytilus edulis Linnaeus, 1758 and *Mytilus californianus* Conrad, 1837 are two species of mussels which occur on the west coast of North America. *Mytilus edulis* is commonly found in bays and on semi-exposed coasts while *Mytilus californianus* is found only on exposed coasts (HARGER, 1967). Association of these species is assumed to be spurious since *M. edulis* and *M. californianus* are so similar. It has been suggested this coexistence is maintained by storms and selective predation which continually provide new surfaces for recolonization (HARGER & LANDENBERGER, 1971; HARGER, 1972).

In quiet bays, *Mytilus californianus*' exclusion has been attributed to physiological and competitive factors. The physiological inability of larval *M. californianus* to withstand salinity stress has been proposed as a possible determinant of exclusion (YOUNG, 1941). A very wide range of salinity tolerance has been shown for larval *M. edulis* (BAYNE, 1965).

HARGER (1968) suggests that exclusion of *Mytilus californianus* is caused by the upward crawling behavior of *M. edulis* which smothers the less mobile *M. californianus* under accumulating silt and pseudofeces. In bays with swift currents, less silt accumulates and *M. californianus* is found (HARGER, 1972).

However, there are several aspects of the distribution of *Mytilus californianus* which cannot be fully explained by either competitive or physiological factors. First, *M. californianus* is often not even found in bays of normal salinity (e.g. MACGINITIE, 1935). Second, Harger assumes *M. californianus* cannot compete after settling, yet shells of juvenile *M. californianus* are not found within mussel clumps from bays (PETRAITIS, 1974). Finally, settlement studies in bays never report juvenile *M. californianus* even on clean surfaces without *M. edulis* (e.g. GRAHAM & GAY, 1945; REISH, 1964).

If a population of a species is being held below the carrying capacity of the environment because of another species, there is a selective advantage to any gene which reduces or eliminates this sharing of resources (COLE, 1960). It would seem probable that the partition of the available space by *Mytilus edulis* and *M. californianus* can be explained by this hypothesis.

Both species are known to settle selectively. *Mytilus edulis* sets sequentially, first on filamentous algae and then into adult clumps (BAYNE, 1964). Without noting whether settlement is primary or secondary, small *M. edulis* have been found along the byssal threads of adults (SEED, 1969; DAYTON, 1971), on a variety of algae (COLEMAN, 1940; DEBLOK & GREELAN, 1958; SEED, 1969) and on newly exposed surfaces (MOORE, 1939). *M. californianus* have been reported to settle on barnacles (DAYTON, 1971), on old mussel shells (YOUNG, 1946) and on newly exposed surfaces (SHELFORD *et al.*, 1935).

Work was undertaken to clarify whether or not the species' differences in juvenile mussel distributions exist and if these differences could account for the known differences in adult distributions.

METHODS

All work was done at Crystal Pier in Pacific Beach and on a floating dock in Mission Bay unless otherwise stated. Both locations are in the San Diego, California area.

Distributional differences were examined by sampling twenty-six quadrats. Sampling was done by scraping off all mussels within a square which was approximately 56 square centimeters. Mussels were sorted by species and size. Since *Mytilus edulis* can grow to 7 mm in one month (COE, 1945) and *M. californianus* to 4 mm in one month (COE & FOX, 1942), mussels under 5 mm were designated as juveniles. Three of the samples were taken from the north jetty at the entrance of Mission Bay. Sampling dates, locations, and the number of adult and juvenile mussels per sample are given in Table 1.

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Juvenile differences in distribution were also examined by nearest neighbor methods. Pilings at Crystal Pier were chosen at random from those that could be reached at low tide. Sampling was done on July 2 and 3, August 16 and 27, September 15 and October 13, 1973. The September fifteenth data were taken at Scripps Institution of Oceanography Pier. A plumb line was placed on each piling. The species of all juvenile mussels that intersected the line and

the species of the next nearest mussel were recorded. Data collected after July 3, 1973 included the size of the nearest neighbor and the surface to which the juvenile mussel was attached.

In order to determine the relative abundance of substrate types, points along the plumb line were chosen at random. The surface type at each point and size of the nearest mussel were noted. These data were collected on February 8, 1974.

To test for the effects of adult mussels on settlement behavior, plastic ice cube trays with transplanted mussels were placed on the exposed coast and in the bay. The first experiment was conducted from July 6, 1973 to October 27, 1973. Five mussels of either species were placed in each cube. Four cubes were allocated for each of the three treatments: pure *Mytilus californianus*, pure *M. edulis*, and no mussels. Trays were covered with Varathane coated 0.63 cm ($\frac{1}{4}$ inch) mesh. Trays on the exposed coast were positioned at the mean tide level. Trays in the bay were suspended from a floating dock, 30 cm below the surface. At the end of the experiment, juveniles present were counted.

A second experiment was conducted from October 28, 1973 to March 6, 1974. In this experiment, seven mussels per cube and eight cubes per treatment were used.

RESULTS

Quadrat samples were analyzed by Spearman rank correlation. The number of juvenile *Mytilus edulis* per quadrat is correlated with the number of adult *M. edulis* per quadrat. Number of juvenile and adult *M. californianus* are also correlated. All other comparisons show no significant correlations (see Table 1).

Nearest neighbor data were tested by two way G test of independence (SOKAL & ROHLF, 1969). Analysis shows occurrence of juveniles depends on the presence of the same species (Table 2). For 129 of the 153 observations in Table 2, the juvenile is touching its nearest neighbor. The choice of substrate also depends on the species of the juvenile. Juvenile *Mytilus californianus* are found almost exclusively on *M. californianus*, while juvenile *M. edulis* are found on all types of surfaces.

Goodness of fit tests of the juveniles' utilization of substrate against the frequency of available substrate show a poor fit for both species (see Table 3, random point comparisons). Neither species settles randomly.

From the random point data, the mean length of the *Mytilus edulis* population (2.3 ± 0.30 cm) and of the *M. californianus* population (3.1 ± 0.77 cm) were estimated.

Table 1

Date, location and number of mussels per quadrat. Spearman rank correlations between abundances are given. Letters J denote juveniles; A, adults; M.e., *Mytilus edulis*; and M.c., *Mytilus californianus*. * $P < 0.01$.

Location and Date	Number of			
	AM.e.	JM.e.	AM.c.	JM.c.
Mission Bay Jetty	11	4	24	8
June 18, 1973	64	31	59	19
	40	2	37	3
Crystal Pier	51	37	20	14
June 18, 1973	73	21	10	5
Crystal Pier	0	0	53	27
July 2, 1973	64	12	35	10
	58	9	23	7
Crystal Pier	36	14	11	1
July 4, 1973	43	19	10	12
Crystal Pier	0	0	23	0
December 9, 1973	1	0	37	25
	1	0	12	6
	52	2	29	6
	44	7	35	10
	0	0	82	28
	1	0	21	4
	44	3	11	0
	45	2	18	4
	38	1	2	0
	0	0	31	0
	2	0	42	15
	0	0	11	0
	15	1	6	0
	0	0	0	0
	0	0	0	0
Correlation coefficients				
	AM.e.	JM.e.	AM.c.	JM.c.
AM.e.		0.880*	0.045	0.259
JM.e.			-0.009	0.272
AM.c.				0.706*

Table 2

Nearest neighbors of juvenile mussels on the exposed coast. Words in parentheses indicate relative levels of mortality observed by HARGER (1967). * $P < 0.01$.
G denotes the G statistic (SOKAL AND ROHLF, 1969).

Base point	Nearest neighbor		G
	M.e.	M.c.	
Juvenile <i>Mytilus edulis</i>	56 (Low)	6 (High)	
Juvenile <i>Mytilus californianus</i>	9 (Low)	82 (High)	106.1*

Table 3

Comparison of substrate preferences of juvenile mussels on the exposed coast. Organisms in the 'other' column are predominantly barnacles. * $P < 0.01$.
Degrees of freedom are denoted by df.

Base point	Substrate utilized			
	M.e.	M.c.	Other Living Organisms	Clear Surface
Juvenile <i>Mytilus edulis</i>	11	5	20	13
Juvenile <i>Mytilus californianus</i>	1	40	5	23
Random point	8	30	12	16
Comparison			df	G
<i>Mytilus edulis</i> versus <i>Mytilus californianus</i>			3	49.81*
<i>Mytilus edulis</i> versus random point			3	33.31*
<i>Mytilus californianus</i> versus random point			3	20.66*

A t-test of the mean length of the *M. edulis* population against the mean length of the *M. edulis* nearest to a juvenile *M. edulis* (0.8 ± 0.14 cm) shows significant differences ($P < 0.01$). Juvenile *M. edulis* are found among smaller *M. edulis* than are found on the average in the population. The same test comparing the mean length of the *M. californianus* population against the mean length of the *M. californianus* to a juvenile *M. californianus* (1.7 ± 0.71 cm) shows no significant differences. Juvenile *M. californianus* are found among *M. californianus* of similar length to those found in the population.

In the transplant studies (Table 4) the total number of mussels which settled in all cubes were counted. The data

were analyzed by a three way G test of independence (BISHOP *et al.*, 1975). Since some cubes were washed away, ten cubes were randomly chosen from each cell to equalize the cell size.

The choice of surface, the surface location and the species of the settler are not independent (Table 4, test 4). However, regardless of the surface, the species of the settler is independent of the surface location (Table 4, test 1). For both *Mytilus californianus* and *M. edulis* settlers, the choice of surfaces is also independent of surface location (Table 4, test 2). Finally, for a given area, either the bay or the exposed coast, the choice of surface depends on the species of the settler (Table 4, test 3).

Table 4

Occurrence of successfully settled juvenile mussels among artificial clumps of adults. Total number of juveniles, based on ten replicates, is given. In parentheses are the expected counts assuming species \times surface independence.

Location of Surface	Species of Settler	Surface		
		M.e.	M.c.	Open
Sea	<i>Mytilus edulis</i>	34 (22.7)	14 (28.0)	8 (5.3)
	<i>Mytilus californianus</i>	0 (11.3)	28 (14.0)	0 (2.7)
Bay	<i>Mytilus edulis</i>	7 (6.3)	8 (9.1)	4 (3.6)
	<i>Mytilus californianus</i>	0 (0.7)	2 (1.0)	0 (0.4)
Tests of Independence		df		G
Test 1. Location \times Species		3		7.38 n.s.
Test 2. Location \times Surface		4		3.31 n.s.
Test 3. Species \times Surface		4		56.68*
in the bay		1		3.21 n.s.
on the coast		1		53.47*
Test 4. Location \times Species \times Surface		7		167.16*

Note that a significant part of the deviations from species and surface independence is due to surfaces located on the coast. In bays, the choice of surface is independent of the species of the settler. On the coast, *Mytilus edulis* settles on *M. edulis* and open surfaces more often and on *M. californianus* less often than would be expected. *M. californianus* settles on *M. californianus* more often and on *M. edulis* and open surfaces less often than would be expected.

DISCUSSION

HARGER (1972) proposed that multiplicity of exposure, the periodicity and species dependent effect of storms, structural complexity of available surface and variation in predation allow for coexistence of *Mytilus edulis* and *M. californianus* on the exposed coast. While this may be the case in adult mussel populations, my observations suggest that very different substrates are acceptable for juveniles of these species.

On the coast, juvenile *Mytilus edulis* appear among *M. edulis* of a similar age or among other organisms such as barnacles. Juvenile *M. californianus* are found almost exclusively among older, more diverse (in length) clumps of *M. californianus*.

It is difficult to determine whether species differences in juvenile distribution are due to selective juvenile mortality, selective settlement, or both. Many claims of selective settlement have been based on inferences from the distribution of spat and the possibility of selective juvenile mortality has been ignored.

The only study comparing mortality of *Mytilus edulis* and *M. californianus* used large mussels (HARGER, 1967). Assuming for the moment that juvenile and adult mussel mortality are similar, the mortality differences described by Harger could not explain the distribution of juveniles observed in Table 2.

In exposed coastal areas, Harger found *Mytilus californianus* suffered higher mortality while *M. edulis* suffered lower mortality in mixed clumps than in pure clumps (HARGER, 1967, see Tables 94, 95 and 97). If mortality were the cause of differences in juvenile distribution, then the cell frequencies for juvenile *M. californianus* in Table 2 would be reversed. The distribution of juvenile mussels does not seem to be simply due to differences in mortality.

While differences in juvenile distributions may be maintained by selective settlement, the important question is whether or not these differences promote the association of *Mytilus edulis* and *M. californianus* on the coast. Lack of negative correlation between adults (Table 1) suggests adult mussels do not maintain small, pure clumps. It would seem that historical events randomize the mussel distribution and eliminate the juvenile differences. In spite of these events, differential juvenile settlement may allow each species a recruitment refuge, thus promoting co-existence by insuring recruitment.

In bays, juvenile *Mytilus californianus* are rarely found. HARGER (1968) proposes that the exclusion of *M. californianus* from bays is the result of competitive interactions with *M. edulis*. Yet the absence of juveniles even among the transplanted *M. californianus* suggests that exclusion is

not maintained by competition. The lack of juvenile *M. californianus* could be explained more simply in terms of low rates of successful recruitment into bays because of high larval mortality.

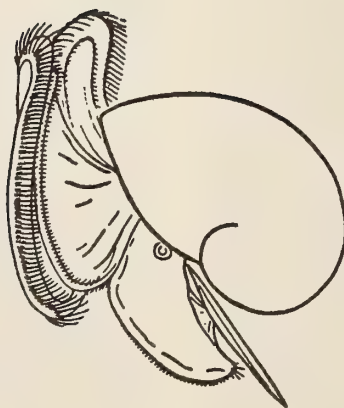
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Flight Responses of Three Congeneric Species of Intertidal Gastropods (Prosobranchia : Neritidae) to Sympatric Predatory Gastropods from Barbados

BY

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INTRODUCTION

LEWIS (1960) RECORDS AT LEAST 3 species of gastropods belonging to the genus *Nerita* inhabiting the mid to high rocky intertidal shores of Barbados; the Bleeding Tooth Nerite, *Nerita peloronta* (Linnaeus, 1758), the Variegated Nerite, *Nerita versicolor* (Gmelin, 1791), and the Checkered Nerite, *Nerita tessellata* (Gmelin, 1791). These grazing gastropods are broadly distributed throughout the Caribbean province from southern Florida and the Bahamas to as far south as Para, Brazil (RUSSELL, 1941). The 3 species show a well defined zonation with only a little overlap (HUGHES, 1971). Highest on the shore is *N. peloronta*, usually found on the surface of large seaward facing boulders above mean high water spring (MHWS) in exposed situations where they receive the full force of the surf; however, they are seldom submerged. *Nerita versicolor* generally is found at the same levels, but extending slightly below MHWS; it is most often limited to more protected areas. Lowest on the shore is *N. tessellata*, often, but not always, found submerged in small rocky tidal pools from mean low water (MLW) to the mean tide level (MTL). Hughes noted that *N. tessellata* has a mean density throughout the zone of 93.2 ± 20.8 SE/m² with the density increasing from the seaward to the landward edges; also that it generally prefers open shaded areas or the undersides of flat rocks.

There is a paucity of information concerning the behavior and ecology of these species. STEPHENSON & STEPHENSON (1950) described their zonation in the Florida Keys. LEWIS (1960) provided a description of zonation patterns and some aspects of their reproductive biology in Barbados. He also gave evidence for evaporative cooling in *Nerita tessellata* (LEWIS, 1963). KOLPINSKI (1964) stud-

ied the growth and life histories of these 3 species in Florida. In addition, population energy budgets were compiled for the 3 species of *Nerita* found on Barbados (HUGHES, 1971).

Presently there is relatively little known concerning possible predator-prey relationships between the species of *Nerita* and sympatric species of carnivorous gastropods. In fact, there have been no reports of predator-induced escape or avoidance behavior in the nerites in general, although representative species of most other families of archaeogastropods have been studied extensively (see ANSELL, 1969, for a general review).

During the month of January for 3 consecutive years from 1975 through 1977, we had the opportunity to make observations on predator-induced behavior of the 3 species of *Nerita* from Barbados both in the field and under laboratory conditions. We were especially interested in the effect of the high intertidal carnivorous thaidid gastropod, *Purpura patula* (Linnaeus, 1785) on the behavior of the nerites. This carnivore has been implicated by LEWIS (1960) as a predator of the chiton, *Acanthopleura granulata* (Gmelin, 1791) and the barnacle, *Tetraclita squamosa* (Bruguère, 1789), and overlaps the distribution of the 3 species of nerites in the rocky intertidal, from mean sea level (MSL) to a few feet above MHWS (LEWIS, *op. cit.*).

FIELD OBSERVATIONS

Observations on gastropods were made at 2 small indentures on the NE exposed rocky coast of Barbados, River Bay (13°19'N; 59°36'W) and Little Bay (13°18'N; 59°35'W). Initially observations were made on *Nerita tessellata* that were found clustered in small (0.1 to 0.5 m diameter) tidal pools at low tide. Small pools that contained approximately 10-15 nerites were chosen for such observations. Specimens of predatory species of gastropods

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Table 1

The ability of different species of gastropods to elicit an escape response in the Checkered Nerite, *Nerita tessellata* Gmelin, in the field

Species ¹	Response ²	Species ¹	Response ²
<i>Thais haemastoma floridana</i> (Conrad, 1893)	XXX	<i>Bursa thomae</i> (Orbigny, 1842)	X
<i>Thais rustica</i> (Lamarck, 1822)	XXX	<i>Bursa granularis cubaniana</i> (Orbigny, 1842)	X
<i>Thais deltoidea</i> (Lamarck, 1822)	X	<i>Coralliophila caribaea</i> (Abbott, 1958)	X
<i>Purpura patula</i> (Linnaeus, 1758)	XXX	<i>Conus mus</i> (Hwass, 1792)	X
<i>Leucozonia nassa</i> (Gmelin, 1791)	XX	<i>Charonia variegata</i> (Lamarck, 1816)	X
<i>Leucozonia ocellata</i> (Gmelin, 1791)	XX	<i>Cittarium pica</i> (Linnaeus, 1758)	X

¹At least five replicate observations were taken using different specimens of each species of snail. The addition of a nerite to an adjacent pool of snails served as control.

²X: response similar to control, little or no movement by the nerites; XX: activity evident, a few to many of the nerites crawled out of the pool by 15-20 minutes; XXX: full response, most of the nerites crawled out of the pool within 20 minutes.

were introduced to the center of the pool. Table 1 qualitatively records the ability of various intertidal and subtidal gastropods to elicit an avoidance or escape response in *N. tessellata*. The strongest response, *i.e.*, the nerites actually leaving the tidal pool in an arbitrarily determined time of 20 minutes, was most apparent in the presence of 3 species of thaidid gastropods, *Purpura patula*, *Thais haemastoma floridana* (Conrad, 1893), and *Th. rustica* (Lamarck, 1822); also to a lesser extent by the fascioliariids, *Leucozonia ocellata* (Gmelin, 1791) and *Leucozonia nassa* (Gmelin, 1791). No response was elicited by herbivorous forms or by gastropods that are subtidal by nature. The behavioral response of *N. tessellata* to the presence of carnivorous gastropods was elicited not by contact but by distance chemoreception. Initially the nerites elevated the anterior end of the shell exposing the head. The long pigmented cephalic tentacles began to flail back and forth in a violent manner; and then the snails exhibited increased locomotory activity which often, but not always, resulted in their leaving the pool of water. Many of the "escaped" nerites were so highly activated that they often moved a distance of 10 to 30 cm from the edge of the pool before coming to rest. The bottom of some small tidal pools held a few millimeters of fine sand, and on rare occasions the presence of a thaidid snail elicited a burrowing response by the nerite into the sand. In no case were any nerites captured or eaten during the course of our observations. However, *Purpura patula*

was observed feeding during low tide on 13 separate occasions on *Nerita tessellata*. In all cases the carnivores were small specimens, averaging about 2.4 cm in length. The nerites had been overturned and the predator was covering the ventral surface with its large foot. Larger specimens (average size, 4.0 cm) were observed feeding on the chiton, *Acanthochiton granulata* (HOFFMAN & WELDON, 1978).

The responses of *Nerita versicolor* and *N. peloronta* to predatory gastropods were difficult to observe in the field at low tide because of their high and dry intertidal position. The open exposed situation of the rocky beach precluded any observations at high tide; therefore any behavioral information had to be collected under laboratory conditions.

EXPERIMENTAL METHODS

The following experiment was designed to test whether the 3 species of *Nerita* in question would demonstrate an escape response to the thaidid gastropod, *Purpura patula*, in the laboratory; and to determine whether such behavior, if evident, was induced by contact or distance chemoreception. Six specimens of either *Nerita tessellata*, *N. versicolor*, or *N. peloronta* were placed into glass finger-bowls (top diameter, 11.5 cm) each of which contained approximately 150 mL of sea water. The *N. tessellata*

ranged in shell length from 1.2 to 1.9 cm; the *N. versicolor*, 1.0 to 2.0 cm; and the *N. peloronta*, 1.4 to 3.3 cm. The *Purpura patula* tested had an average shell length of 2.6 cm. The experiments were designed to collect both descriptive and quantitative data by counting the number of nerites leaving the water in an arbitrarily determined time of 30 minutes after adding the predator or an aliquot of sea water that contained the predator's "scent". In order to standardize the procedures the following steps were taken:

1) After being placed in the bowls the snails were allowed to come to rest, usually 15 - 20 minutes before adding the predatory snail; 2) the experiments were performed between 0800 and 1100 Barbados time under the subdued lighting conditions of the laboratory; 3) an additional nerite was added to each of the control bowls in order to mimic the presence of the predator; 4) to test for distance chemoreception, approximately 25 mL of water taken from a container that held one *P. patula* per 100 mL of sea water was carefully added to the fingerbowl that contained nerites. The control for this experiment entailed adding approximately 25 mL of sea water from the intake sea water valve to a bowl of nerites. All data were tested for significance using the Chi-square Test for 2 independent samples (SIEGEL, 1956).

EXPERIMENTAL RESULTS

Statistically significant data were obtained demonstrating that the presence of *Purpura patula* would elicit an escape response in all 3 species of nerites tested (Table 2). Locomotory activity was exhibited in both experimental and

control bowls; this was most apparent with both *Nerita versicolor* and *N. peloronta*. As high intertidal forms, the act of being submerged stimulates them to activity, so it was not surprising to observe such activity under experimental conditions. All 3 species displayed tentacular flailing in the presence of *P. patula*, a phenomenon that was not evident under control conditions. Since the specimens of *P. patula* that were used in these experiments did not move, but remained attached to the center of the bowls, it appeared that contact was not necessary to trigger the response in any of the species.

The ability to react positively to the "scent" of *Purpura patula* was demonstrated most strongly by *Nerita tessellata* in the water experiments. Although all 3 species of nerites demonstrated some capacity to react to this "scent water", e.g., heightened cephalic tentacular flailing, only *N. tessellata* data were statistically significant at the 0.05 level and beyond (Table 2). The lack of significance in the response of *N. versicolor* and *N. peloronta* may be a function of small sample size. Also, since these last 2 species would never encounter the still water conditions of the tidal pool, but only the surges of the tide, their responsiveness to a predator may be impaired or diminished under such experimental conditions.

Nerita versicolor alone demonstrated a strong negative response to light in that all the snails that emerged from the water in the bowls would do so on the side opposite the incident light. If the bowls were rotated 180°, positioning the active snails immediately before the light, the directional movement would be abruptly changed by 180°; in fact, the nerites often crawled back into the water and exited from the opposite side of the bowl.

Table 2

Summary of the ability of *Purpura patula* or water containing the "scent" of *Purpura patula* to elicit an escape response in three species of *Nerita* from glass fingerbowls

	No. of nerites in expt. bowls at T ₀	No. to leave bowls at T ₃₀	No. of nerites in control bowls at T ₀	No. to leave bowls at T ₃₀	Chi-square
<i>Purpura patula</i>					
<i>Nerita tessellata</i>	144	126	126	64	41.75 ³
<i>Nerita versicolor</i>	72	72	84	73	8.27 ³
<i>Nerita peloronta</i>	54	50	42	32	3.86 ³
<i>Purpura patula</i> water					
<i>Nerita tessellata</i>	84	59	72	18	29.88 ³
<i>Nerita versicolor</i>	72	70	72	63	3.53 ³
<i>Nerita peloronta</i>	42	41	42	36	2.49 ³

³The difference between the experimental and control group is significant ($p \leq 0.05$) when the Chi-square is greater than 3.840.

DISCUSSION

The 3 species of Barbadian nerites exhibit escape of flight behavior that is similar to many trochid gastropods (CLARK, 1958; FEDER, 1963; YARNALL, 1964; HOFFMAN & WELDON, 1978). There was no qualitative difference in the behavioral response of the 3 congeners to *Purpura patula*. The fact that no shell twisting or rotating was shown by any of the nerites gives strength to the argument raised by Hoffman & Weldon that such behavior may serve as an additional adaptation to contact-induced flight behavior as is the case in the top shell, *Tegula excavata* (Lamarck, 1822).

It appears that submergence and light, and perhaps even moving water, may play significant roles in either stimulating or increasing the locomotory behavior of high intertidal forms like *Nerita versicolor* and *N. peloronta*, and should not be overlooked in studies dealing with predator-prey interactions. *Nerita versicolor* may be similar to the Kenyan nerite, *Nerita plicata* (Linnaeus, 1758), which orients itself in the intertidal by alternating positive and negative phototaxes during the morning and afternoon hours of the day (WARBURTON, 1973). Certainly further observations are necessary before we can determine what cues these high intertidal snails use to avoid predation and maintain their position on the beach.

The relatively strong response of *Nerita tessellata* to *Purpura patula*, as well as to other sympatric thaidid and fascioliid gastropods has ramifications in the predator-prey interactions of these species. The fact that *P. patula* can be observed feeding on *N. tessellata* in the field gives credence to this argument. However, more ecological data are needed before any definitive role of the nerites in the diet of these carnivores can be assigned.

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Winter Reproduction in the Gastropod *Nassarius trivittatus*

BY

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INTRODUCTION

THE ROLE OF TEMPERATURE in triggering reproductive activity in marine invertebrates has been widely discussed (see KINNE, 1970). There often seems to be a critical minimum temperature required to stimulate spawning. *Nassarius obsoletus*, for example, the common mud snail, completes gametogenesis 2-6 months prior to the onset of reproductive activity (SASTRY, 1971; SCHELTEMA, 1967) but deposition of egg capsules is apparently delayed until a critical temperature is reached (SASTRY, 1971). Similarly, *N. trivittatus* has been reported to initiate breeding as temperatures rise in the late spring, when water temperatures are 8°-13°C (SCHELTEMA and SCHELTEMA, 1964). However, egg capsules of this species were deposited in a flowing sea water system in the laboratory through December. Since temperature requirements for spawning are generally correlated with temperature requirements for successful embryonic and larval development (KINNE, 1970; THORSON, 1950), the ability of *N. trivittatus* embryos to develop at winter sea water temperatures was examined in the laboratory.

Nassarius trivittatus has been reported on the east coast of the United States from S. Carolina to the Gulf of St. Lawrence, from shallow water and deep water out to the continental shelf (SCHELTEMA & SCHELTEMA, 1964). *Nassarius obsoletus*, the comparison species for this paper, is common in shallow water from Florida north to the Gulf of St. Lawrence (SCHELTEMA, 1967).

MATERIALS AND METHODS

Fifteen *Nassarius trivittatus* dredged in Buzzard's Bay, Massachusetts on October 8, 1973, were held in a sea water table, the bottom of which was covered with mud. Dead fish and pieces of quahogs (*Mercentaria mercenaria*) were occasionally provided as food. The water flowing through the table was pumped from Great Harbor, Woods Hole, Massachusetts, and was within 1°C of the actual field temperatures monitored by the Woods Hole Oceanographic Institution at sixteen feet depth in the harbor. Measure-

ments on egg capsules deposited were made at 50X, and those on eggs and larvae were made at 100X.

Capsules were collected shortly after spawning by carefully removing them from the sides of the water table. Undamaged capsules were placed in perforated plastic petri dishes which were then suspended in the water table. The egg capsules of *N. trivittatus* have been described and figured by SCHELTEMA & SCHELTEMA (1964).

OBSERVATIONS

Nassarius trivittatus sporadically deposited egg capsules in large numbers, from late October until at least mid-December, at which time the water temperature was approximately 7°C. The embryos emerged from the capsules successfully at winter temperatures. Embryos in 4 capsules collected at 11.2°C and suspended in the water table required 27-28 days to hatch at ambient temperatures, which had dropped to 8.8°C at hatching. Ten capsules spawned on November 26 at 9.6°C released veliger larvae after 35-42 days, the last capsules hatching at 5.5°C. Finally, capsules deposited at 7.4°C on December 14 began emptying after 55 days, at a temperature of 3.3°C. Twenty-six capsules collected on December 11 and held in aerated jars of sea water at room temperature (about 21°C) hatched out veligers in 5-7 days, the same pre-hatching developmental period described for summer embryos of this species held at room temperature by SCHELTEMA & SCHELTEMA (1964).

Mean capsule height ($\pm 95\%$ confidence limits) as measured from the base of the capsule to the upper edge of the escape zone was 2.0 mm (± 0.1 mm), and mean capsule width was 1.3 mm (± 0.14 mm) for the 14 capsules measured. Eleven capsules were cut open and found to contain an average of 109.5 embryos each (range=70-144 eggs/capsule), well within the range of values reported by SCHELTEMA & SCHELTEMA (1964). Mean egg diameter was 133 μ m (107 eggs from 7 capsules), and larvae at hatching had a mean shell length of 256 μ m, with a range of 222-291 μ m (112 shells measured from 2 capsules). Size at hatching was larger than that determined by SCHELTEMA & SCHELTEMA (1964 and personal communication) who recorded a

mean shell length of 225 μm and a range of 195-255 μm for larvae from capsules deposited in the summer.

DISCUSSION

The egg capsules of *N. trivittatus* are morphologically very similar to those of *N. obsoletus* (SCHELTEMA, 1962; SCHELTEMA & SCHELTEMA, 1964). The egg size of *N. obsoletus* (166 μm ; COSTELLO & HENLEY, 1971) is slightly greater than that of *N. trivittatus*, and the size at hatching differs correspondingly (about 275 μm for *N. obsoletus* veligers; SCHELTEMA, 1962). The two species initiate reproductive activity at similar temperatures, as discussed below, and both species have a pre-hatch development of about one week at room temperature. (SCHELTEMA & SCHELTEMA, 1964; SCHELTEMA, 1967). Temperature requirements for embryonic development differ markedly, however. Embryos of *N. obsoletus* do not develop below 11-13°C (SCHELTEMA, 1967). In contrast, embryonic development of *N. trivittatus* proceeds at temperatures at least as low as 3.3°C. The successful escape of *N. trivittatus* veligers from egg capsules at 3.3°C indicates that hatching substance (PECHENIK, 1975) is produced by veligers at 3.3°C and is functional at these low temperatures.

Nassarius obsoletus from Rhode Island initiates reproductive activity in the laboratory at about 10°C (PECHENIK, *et al.*, in press), one to several °C below the minimum temperature at which embryonic development proceeds noticeably (SCHELTEMA, 1967). SASTRY (1971) also recorded egg capsule deposition at 10°C by *N. obsoletus* collected from Beaufort, N. Carolina. Embryos deposited at this temperature in the field are probably exposed to higher temperatures during at least part of each tidal cycle due to intertidal placement of the egg capsules (SCHELTEMA, 1967), and water temperatures warm up quickly after egg capsule deposition commences. Capsule deposition is completed by late August in all populations, while water temperatures are still high (JENNER, 1956). The timing of reproductive activity in *N. obsoletus* is thus well attuned to embryonic temperature requirements and conditions in the intertidal zone. Similarly, the ability of its embryos to develop at low temperatures may be an important factor in allowing *N. trivittatus* to occur as far north and at the depths that it does. The ability of *N. trivittatus* larvae to feed and grow at winter temperatures remains to be examined.

Whether subtidal individuals of *N. trivittatus* continue to deposit egg capsules during the winter in the field is unknown, although egg capsule deposition in the fall was

observed by SCHELTEMA & SCHELTEMA (1964) at Barnstable Harbor, Massachusetts. Not all *N. trivittatus* seem to breed at low temperatures; several hundred snails dredged from Buzzard's Bay in 10-15 m of water in mid-November failed to deposit any egg capsules when held at field temperatures during a three-week observation period, November 14-December 6.

SUMMARY

1. *Nassarius trivittatus*, previously reported to breed only in the spring and fall, is capable of producing egg capsules at least until mid-December, at a water temperature of 7.4°C.
2. *Nassarius trivittatus* embryos can develop at winter water temperatures and escape from their egg capsules at temperatures at least as low as 3.3°C. The reproductive physiology of *N. trivittatus* is thus well correlated with the geographical and depth ranges of this species.

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METHODS & TECHNIQUES

Laboratory Cultivation

of *Haminoea solitaria* (Say, 1822)
and *Elysia chlorotica* (Gould, 1870)

BY

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(1 Plate)

INTRODUCTION

OPISTHOBRANCH MOLLUSKS are readily collected in the field, easily maintained in the laboratory, show a variety of behavioral patterns, and possess large neurons. Consequently, they are used in studies on the neural correlates of behavior.

Species in which the neural mechanisms underlying specific behavioral patterns have been studied include the nudibranchs *Hermisenda crassicornis* (Eschscholtz, 1831) (ALKON, 1974a, 1974b, 1975) and *Tritonia diomedea* Bergh, 1894 (WILLOWS, DORSETT, & HOYLE, 1973a, 1973b; HOYLE & WILLOWS, 1973; DORSETT, WILLOWS & HOYLE, 1973), the notaspidean *Pleurobranchaea californica* MacFarland, 1966 (DAVIS & MPITSOS, 1971; DAVIS, MPITSOS, SIEGLER, PINNEO, & DAVIS, 1974), and the anaspidean *Aplysia californica* Cooper, 1863 (see review by KANDEL, 1976). Recent work on the neurological basis of behavior in opisthobranchs, with emphasis on *Aplysia*, is reviewed by KANDEL (1976); see also Willows' review of learning in gastropods (WILLOWS, 1973).

Research on the development of opisthobranch sensory networks in terms of morphology, neurophysiology, and behavior depends on standardizing techniques for laboratory cultivation of these mollusks. Detailed studies are

available on larval development and metamorphosis in a number of opisthobranch species. Notable among these are studies by Thompson on *Tritonia hombergi* Cuvier, 1803 (THOMPSON, 1962), *Cadlina laevis* Linnaeus, 1767 (THOMPSON, 1967), and *Adalaria proxima* ALDER & HANCOCK, 1854 (THOMPSON, 1958), by Tardy on *Aeolidiella alderi* Cocks, 1852 (TARDY, 1970), and by Bonar and Hadfield on *Phestilla sibogae* Bergh, 1905 (BONAR & HADFIELD, 1974). Of the opisthobranch species used in neurophysiological research only *Aplysia californica* Cooper, 1863 (KRIEGSTEIN, CASTELLUCCI & KANDEL, 1974) and *Aplysia brasiliana* Rang, 1828 (STRENGTH & BLANKENSHIP, 1978) have been reared through at least one generation in the laboratory.

This paper describes methods developed to establish laboratory strains of two opisthobranch mollusks, *Haminoea solitaria* (Say, 1822) and *Elysia chlorotica* Gould, 1870 for the purpose of studying neural correlates of behavior in larval, juvenile, and adult stages reared under defined environmental conditions.

Haminoea solitaria, a small infaunal species of the Order Cephalaspidea, Family Atyidae, burrows just under the surface of fine-grained sediments in protected areas of shallow brackish and salt water from Massachusetts Bay to Georgia (Johnson, 1934). The natural history of this species is poorly known. Early observations on the embryology and general biology of *H. solitaria* were made at Woods Hole, Massachusetts by SMALLWOOD (1904a, 1904b). Our observations on timing of egg laying, appearance of the egg mass, and number of eggs per capsule agree with Smallwood's earlier descriptions.

Elysia chlorotica, a member of the Order Sacoglossa, Family Elysiidae, is distributed in shallow salt and brackish water from Nova Scotia to North Carolina (BAILEY & BLEAKNEY, 1967; CLARK, 1975; FRANZ, 1970; GOULD & BINNEY, 1970). Unlike most Elysiidae, which have narrow food preferences, *E. chlorotica* is found on a variety of algae, including species of Cladophorales, *Enteromorpha clathrata* Roth, the xanthophyte *Vaucheria*, and the halophyte *Ruppia*, as well as in patches of *Zostera marina* Linnaeus and on peat banks of channels (BAILEY & BLEAKNEY, 1967; CLARK, 1975; PFITZENMEYER, 1960; RUSSELL, 1946, 1964, present study). *Elysia chlorotica* is dark green in color, due most likely to the presence of chloroplasts, which in *Elysia hedgpethi* Marcus, 1961 and *Elysia viridis* (Montagu, 1804) are taken up from the algal food and stored in a functional condition in cells of the digestive gland (GREENE, 1970).

Elysia chlorotica is highly tolerant of variations in physical environmental factors. PFITZENMEYER (1960) found it in Chesapeake Bay, Maryland at temperatures as low as 4.3°C and salinity of 10.5‰. BAILEY & BLEAKNEY (1967) studied its distribution in salt marshes of the Minas Basin,

Nova Scotia, where the animals are exposed to tides ranging to 11.6 m and to wide variations in temperature and salinity. In the present study 2 laboratory populations of *E. chlorotica*, one maintained at ambient winter seawater temperature down to -1.0°C and the other at $18^{\circ}\text{--}26^{\circ}\text{C}$, showed good survival for several months (salinity = 32‰).

Both *Haminoea solitaria* and *Elysia chlorotica* are relatively common in salt marshes and estuaries of the northeastern United States. Such estuarine forms tend to be eurytopic with respect to physical environmental factors, making them good candidates for successful cultivation in the laboratory.

MATERIALS AND METHODS

1. *Haminoea solitaria*

In mid-September 1976, 6 adults were collected at low tide by sieving the top 5 cm of mixed fine sand and mud along the upper part of the bank of the main tidal channel at the back of Little Sippewisset Marsh, Falmouth, Massachusetts (lat. $41^{\circ}34'\text{N}$, long. $70^{\circ}38'\text{W}$, water temp. $19^{\circ}\text{--}20^{\circ}\text{C}$). To induce copulation and egg laying the animals were maintained as a group in a 190 x 100 mm glass dish containing 2 cm of sand from the habitat, held at ambient water temperatures of $18^{\circ}\text{--}20^{\circ}\text{C}$. Water in the dish was changed daily and the sand stirred to prevent the development of anaerobic conditions.

Egg masses were washed in $0.22\text{ }\mu\text{m}$ Millipore-filtered (MPF) seawater and placed in a glass dish with about 100 mLs of MPF seawater. The eggs were maintained at the same temperature at which they were deposited ($18^{\circ}\text{--}20^{\circ}\text{C}$). To reduce bacterial contamination the water was changed daily and the glass surfaces cleaned in hot tap water.

2. *Elysia chlorotica*

In mid-October 1976, a population of thousands was discovered in a salt marsh adjacent to the tidal inlet at Menemsha Pond, Martha's Vineyard, Massachusetts (lat. $41^{\circ}21'\text{N}$, long. $70^{\circ}46'\text{W}$, water temp. $16^{\circ}\text{--}18^{\circ}\text{C}$). The animals were found in tidal channels, primarily on fine sand and mud overlain by marsh detritus, or under large mats of filamentous green algae, mainly *Cladophora* spp. and *Enteromorpha* spp., which lined the channel banks. Areas of coarser ocean beach sand contained fewer individuals.

Approximately 100 individuals were collected at random and maintained in a slow flow-through seawater system at ambient temperatures (18°C and below). Both filamentous algae and marsh detritus were provided as food.

Egg laying, which virtually ceased below 15°C , was induced by placing 20 adults in a 12-L recirculating aquarium held at $18^{\circ}\text{--}24^{\circ}\text{C}$. Algal food was provided. Egg masses were removed intact from the aquarium walls and maintained as described for *Haminoea* eggs, but at temperatures of $18^{\circ}\text{--}24^{\circ}\text{C}$.

3. Methods for Handling Larvae.

Both species hatched out as veligers. Newly-hatched veligers swimming near the water surface were washed by serially transferring them with a Pasteur pipet to MPF seawater of the same temperature. On the third transfer 50 veligers were counted out, using a dissecting microscope, into 3 to 5 replicate 100 x 20 mm Pyrex petri plates, each containing fifty mLs of MPF seawater, for a density of one veliger per mL. All plates were kept covered. To prevent veligers from becoming trapped in the surface film several flakes of cetyl alcohol were sprinkled on the water surfaces (HURST, 1967). Each culture was fed 2.5×10^4 cells per mL of each of the unicellular algae *Isochrysis galbana* Parke and *Monochrysis lutheri* Droop. Larvae were transferred daily by pipet to plates with clean water and fresh food. All cultures were maintained at room temperatures of $18^{\circ}\text{--}24^{\circ}\text{C}$. Growth rates were determined by weekly measurements of shell length of randomly selected individuals at 200x, using a calibrated ocular micrometer.

The primary films used to induce metamorphosis were grown by placing small amounts of sediment from the adult habitat in clean 100 x 20 mm Pyrex petri plates filled with MPF seawater. Under conditions of strong daylight and frequent water change the bacteria and diatoms from the sediment spread out into a thin film on the glass. After 1-2 weeks growth the sediment was discarded, the plates rinsed to remove loose particles, and clean seawater and late veligers added.

Bacteria-free mono-algal cultures of *Isochrysis galbana* and *Monochrysis lutheri* were grown in $0.45\text{ }\mu\text{m}$ MPF seawater enriched with Guillard's f/2 medium and autoclaved (GUILLARD, 1975). Only cultures in the log phase of growth were fed to larvae.

RESULTS AND DISCUSSION

1. *Haminoea solitaria*

Haminoea solitaria was collected at the end of its reproductive season in Little Sippewisset Marsh, as no adults were found in the marsh after mid-September. The adult retains a thin, white, inflated shell which in life is partly covered by parapodia. Shell length and width of the 6

adults collected ranged from 6.1 x 7.3 mm to 8.5 x 5.4 mm, slightly smaller than the average shell size (10 x 7 mm) reported by SMALLWOOD (1904b). The anterior end of the animal, consisting mainly of the cephalic shield, could be extended to nearly double the shell length.

Egg masses began to appear on the sand surface after 2 days in the laboratory. Egg laying occurred frequently at or just prior to dawn, as eggs were often discovered in the 1- to 4-cell stage in early morning. However, masses were deposited during the day as well. The egg mass, a gelatinous sphere about 2 cm in diameter, is attached to sand grains by a thin stalk 1 to 2 cm long. Eggs, 1 per capsule, were embedded in the matrix only around the periphery of the sphere. Rough counts of eggs in 5 replicate 1 mm² areas, multiplied by the calculated surface area of each of 3 egg masses, gave estimates of 2 000-3 000 eggs per mass. Veligers emerged in 7 days at 18°-20°C. Hatching continued for about 3 days as the egg masses progressively disintegrated. The sticky organic matrix, which became semi-fluid during hatching was observed to support a large population of bacteria and small invertebrates such as ciliates and nematodes. These organisms may aid hatching by feeding on the gelatinous part of the egg mass, as suggested by HARRIS (1973) for the hatching of nudibranch veligers. Breakdown of gelatinous egg masses may also be facilitated by the production of enzymes by the developing larvae, as hypothesized by DAVIS (1968).

Newly-hatched veligers, possessing a type 1 shell (THOMPSON, 1961), swarmed just beneath the water surface. Each veliger was characterized by a prominent, roughly triangular black spot (about 20 x 18 µm) near the larval anus. This pigmented spot occurs in other cephaspid veligers, where it has been identified as a larval kidney (HURST, 1967; THORSON, 1946). Shell length of newly-hatched veligers was 150.6 ± 3.3 µm (n=35). Statocysts were present at hatching and eyes appeared 6 to 7 days later.

By ten days post-hatching most larvae swam just above the plate bottom, occasionally pressing the velar lobes against the glass. A few veligers reached maximum shell length (236 µm) and had well developed propodia by 12 days post-hatching, when the first pediveliger was observed. However, veligers did not begin to metamorphose on a primary film until 20 days post-hatching. Metamorphosis (at shell lengths of 217-236 µm) was accomplished by slow resorption of the velar lobes over a period of 48 hours. Development of the adult radular feeding apparatus soon after velum loss allowed juveniles to feed on the primary film.

To determine if metamorphosis was dependent on a primary film, all 20-day veligers were divided into 3 equal groups: one group was exposed to a 2-week primary film,

the second to sand grains from the adult habitat, and the third to clean glass. Metamorphosis was dependent on the presence of microorganisms from the adult habitat (Table 1). Seventy percent of all remaining 27-day old veligers metamorphosed when exposed to a primary film for two weeks. In summary, 43% of the total number of veligers (n=185) exposed to a primary film between days 20 and 41 post-hatching successfully metamorphosed.

Table 1

% metamorphosis in *Haminoea solitaria*
on days 20-27 post-hatching

Primary film	37% (n = 61)
Sand grains	13% (n = 62)
Glass	0% (n = 62)

Post-metamorphic shell growth was heterostrophic. Seven-day juveniles measured to 270 µm in shell length, increasing to 350 µm by 28 days. The cephalic shield and eyes were well-developed by 1 week. By 28 days the protoconch was noticeably sunken and the shell had assumed the adult inflated form.

Several problems were encountered in maintaining the juveniles, resulting in a poor post-settlement rate of survival. First, rapid growth of the primary film fouled the shells, entrapping the juveniles. Second, it was not possible to wash all potential predators and competitors, mainly small crustaceans, from the sand provided as a food supply for the juveniles. Although larval survival (about 50% to the pediveliger stage) and percent metamorphosis (43%) were relatively high, dietary preferences in juveniles and adults need to be accurately determined and better handling procedures developed before this species can be reared in large numbers in the laboratory.

2. *Elysia chlorotica*

The average body length of a sample of 100 adults, measured from a point halfway between the tentacles to the tip of the tail, was 2.28 cm (range=1.09 to 3.36 cm). No very small *Elysia* were found by microscopic examination of sediment samples in October and November.

Elysia chlorotica (Figure 1) will readily lay eggs in the laboratory, provided the average temperature remains above 15°C; an exception was one very small egg mass laid at 9°C. Photoperiod may also affect egg laying; the laboratory was maintained on a 12 hour light: 12 hour dark cycle, closer to summer than to winter photoperiods. Twenty

adults kept at room temperature and fed filamentous green algae produced 30 egg masses in 5 weeks. Egg masses are whitish in color and deposited in either flat counterclockwise spirals, or, more frequently, in an irregular pattern. Egg strings are attached along their entire length to the substratum; in the laboratory, eggs were attached to the aquarium wall except once when the substratum was filamentous green alga. Spiral egg masses were slightly flattened along 1 axis, and usually consisted of 3 to 4 turns. Eggs were packed randomly within the egg string, generally 1 egg per capsule, occasionally 2 to 3 per capsule. Egg capsules were elliptical in shape. Ends of the egg strings tapered and often contained a few empty capsules. The number of eggs in each of 7 egg masses was estimated by first measuring the uncoiled length of the egg string with a ruler, then counting all eggs in 5 replicate 1 mm long sections selected at random. The average number of eggs per mm multiplied by the length of the egg string in mm gave the approximate number of eggs in the string. The estimated number of eggs per mass varies with the length of the egg string (Table 2). In one particularly large egg mass

Table 2

No. of eggs per egg mass in <i>Elysia chlorotica</i>				
Dia. egg mass (mm)	Width (mm)	Length (mm)	\bar{X} no. of eggs across string	Est. eggs
7.5 × 7.5	0.8	30	8.0	3,360
10.1 × 10.0	0.8	75	9.0	10,200
Irregular	0.9	76	9.8	9,979
Irregular	1.2	81	13.0	11,583
14.8 × 12.9	1.2	92	15.6	24,111
Irregular	1.2	96	13.6	19,200
Irregular	1.2	131	19.0	48,287

70% of the capsules contained 1 egg, 29+ % contained 2 eggs, and less than 1 per cent contained 3 eggs. Capsules containing more than 1 egg were found in only the largest egg masses. Egg size decreased slightly with increasing

Table 3

Average sizes of eggs and capsules in *Elysia chlorotica*

	egg diam. μm	capsule diam. μm
one egg/capsule	78.4 \pm 2.8 (n = 20)	194.3 \pm 17.1 \times 170.9 \pm 32.8 (n = 20)
two eggs/capsule	75.9 \pm 1.5 (n = 20)	214.8 \pm 5.4 \times 202.5 \pm 5.8 (n = 20)
three eggs/capsule	74.3 \pm 1.8 (n = 3)	230.9 \times 216.4 (n = 1)

numbers of eggs per capsule, and capsule size increased (Table 3).

Shell lengths of newly-hatched veligers did not vary with temperatures between 9°C and 24°C; however, development took longer at lower temperatures (Table 4). Aver-

Table 4

Relationship between T°C and development time in *Elysia chlorotica*

T°C	days to hatching
20° - 24°	6
13° - 15°	8 - 9
9° - 12°	12

age shell lengths varied slightly among samples of veligers from 3 different egg masses allowed to develop at 20°-24°C: 138.5 \pm 4.4 μm , 126.0 \pm 5.2 μm , and 132.4 \pm 4.5 μm , n = 35 each sample. The veliger shell was unsculptured and belonged to Thompson's Type 1 (THOMPSON, 1961).

No chloroplasts were detected by microscopic examination in either the eggs or the newly-hatched veligers of *Elysia chlorotica*. GREEN (1968) did not find chloroplasts in the egg mass of *Elysia hedgpethi*. He suggests that chlo-

Explanation of Figures 1 to 3

Figure 1: Adult *Elysia chlorotica*

Figure 2: Cast larval shell and operculum of *Elysia chlorotica*

Figure 3: Newly metamorphosed juvenile of *Elysia chlorotica*



Figure 1



Figure 2

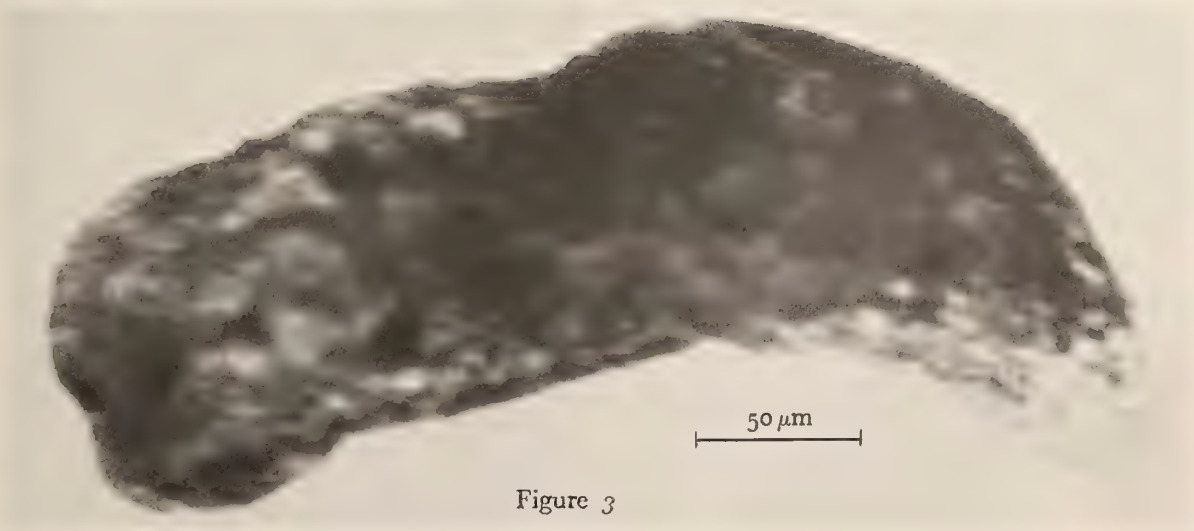


Figure 3

roplasts are taken up anew by each generation (GREEN, 1970). If *E. chlorotica* has functional chloroplasts the juveniles must obtain them when they begin to feed on filamentous algae.

Veligers swam at the surface for the first 10 days post-hatching. Statocysts were present at hatching and eyes appeared on days 5 and 6. Newly-hatched veligers were characterized by a row of black spots in the mantle edge around the shell aperture. From day 9 a band of black spots began to spread from the base of the shell aperture dorsally. By days 12-14 the spots had spread and coalesced, so that the entire veliger, including the foot, appeared black. This pigment always appeared near maximum shell length, 240 μm . No veliger was observed to metamorphose before the body had entirely darkened. Seventy percent of the veligers attained a shell length at which metamorphosis (212 μm) could occur by day 12 post-hatching. Pigmentation development was complete within 2 to 3 more days.

LARVAL REARING EXPERIMENT 1:

Seventy-six percent of veligers survived to day 14 post-hatching in two plates containing initially fifty larvae each. Day 14 veligers were exposed to a variety of materials from the adult habitat: a primary film grown from marsh detritus, filamentous green algae, adult mucus, and adults. On day 28 post-hatching 1 veliger metamorphosed on a primary film. Metamorphosis took 2 days to complete; first the velum was resorbed, then about 24 hours later the shell and operculum were cast (Figure 2), resulting in a rapidly moving, black worm-like juvenile which lacked both tentacles and parapodia (Figure 3).

On day 42 post-hatching half the remaining larvae ($n=37$) were exposed to a 0.1% solution in MPF seawater of the neuromuscular blocking agent succinylcholine chloride (Sigma Chemical Co.) in a filmed plate. BONAR (1976) successfully used this compound to induce metamorphosis in the nudibranch *Phestilla sibogae* Bergh, 1905. The mechanisms of action of this chemical are unknown in invertebrates. Between days 46-55 post-hatching 60.6 of the veligers metamorphosed in the succinylcholine chloride solution as opposed to none in a filmed plate with seawater alone.

LARVAL REARING EXPERIMENT 2:

One out of 55 veligers which survived to day 16 post-hatching metamorphosed on a primary film, prior to any experimental manipulations. Based on growth rate at 20°-24°C and rate of development of pigmentation in veligers, 16 days is probably the earliest that metamorphosis might occur in the field at summer water temperatures.

Day 16 post-hatching veligers ($n=54$) were divided into 3 equal groups. The first group was placed in seawater alone, the second in seawater containing 2mLs of a seawater extract of filamentous algae from the adult habitat, and the third in a seawater solution of 0.1% succinylcholine chloride. All 3 plates had a primary film; the larvae were fed unicellular algae. By 23 days post-hatching 10 of 18 veligers had metamorphosed in the succinylcholine chloride solution, but none in either of the other 2 conditions. On day 23 all remaining veligers were placed in succinylcholine chloride, resulting in a total of 42.4% metamorphosis in that sample of veligers exposed to the chemical.

Length of shells cast at metamorphosis ranged from 211.9 μm to 226.1 μm . Lengths of the extended juveniles ranged from 350-450 μm . No morphological differences were noted between juveniles which metamorphosed with and without succinylcholine chloride. Based on the initial sample of 100 veligers in experiments 1 and 2, total metamorphosis was 15-20%.

Research is currently in progress to find the natural inducer of metamorphosis in *Elysia chlorotica*, as well as to establish rearing techniques for both *E. chlorotica* and *Haminoea solitaria*.

SUMMARY AND CONCLUSIONS

1. The cephalaspid *Haminoea solitaria* and the sacoglossan *Elysia chlorotica* have been reared through metamorphosis in the laboratory.
2. *Haminoea solitaria* metamorphoses in response to a primary film grown from sediments collected in the adult habitat. Veligers begin to metamorphose after 20 days at temperatures of 18°-24°C. The shell is retained in this species.
3. Metamorphosis in *Elysia chlorotica* occurred after a 16-day veliger stage in response to a primary film grown from sediments taken from the adult habitat. The percent of metamorphosed larvae was increased by using a 0.1% solution in seawater of succinylcholine chloride in a plate with a primary film. The shell and operculum are discarded in this species.
4. Because they tolerate wide variation in physical environmental factors and have a relatively short planktonic stage, these estuarine opisthobranchs are good candidates for prolonged cultivation in the laboratory. These two species are being maintained under defined environmental conditions throughout the entire life cycle in order to investigate the development of behavior in connection with the development of the nervous system.

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NOTE ADDED IN PROOF

After the above paper had been accepted for publication, the following relevant publications on opisthobranch culture appeared:

HARRIGAN, JUNE F. & DANIEL L. ALKON

1978. Larval rearing, metamorphosis, growth and reproduction of the eolid nudibranch *Hermisenda crassicornis* (Eschscholtz, 1831) (Gastropoda: Opisthobranchia). Biol. Bull. 154 (3): 430-439; 3 text figs.

KEMPF, STEPHEN C. & A. O. DENNIS WILLOWS

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NOTES & NEWS

Additional Notes

on *Spurilla alba* (Risbec, 1928)
(Mollusca: Opisthobranchia)

BY

GALE G. SPHON

Los Angeles County Museum of Natural History
Los Angeles, California

DURING THE PAST SEVERAL YEARS, Forrest and Roy Poorman have collected opisthobranchs for the Los Angeles County Museum of Natural History, and have care-

fully documented the specimens with 35 mm color slides. Among the many lots donated to the Museum were 3 specimens of *Spurilla alba* (Risbec, 1928) collected in November, 1975. In 1971 this species had been reported from Punta Mita, Nayarit, Mexico, the first record for the Eastern Pacific (SPHON, 1971). Aside from the type locality of Noumea, New Caledonia, it had also been reported from New South Wales and Queensland, Australia (BURN, 1966) and from Tanzania, Africa (EDMUNDS, 1969). Thanks to the efforts of the Poormans, I am now able to report this species from San Carlos Bay, near Guaymas, Sonora, Mexico, a range extension of about 800 km northward in the Eastern Pacific.

Photographs taken of the Nayarit and one of the Sonoran specimens (the other 2 were not photographed and had lost their color in the ethanol they were preserved in) show some variation in coloration. The Nayarit specimen is chalk-white with more intense white speckles covering the cerata and body. The Sonoran specimen has the same basic chalk-white but the speckles are brownish in color and give the animal a pinkish cast. At the base of the rhinophores in the Nayarit specimen is a vermilion-colored ring encircling them like a figure 8. The Sonoran specimen also has this, but there is an orange color that suffuses the lower $\frac{2}{3}$ of the rhinophores. A lighter version of this orange coloration appears between the head tentacles on the Nayarit specimen, but is absent in the Sonoran one.

In the original description, Risbec states that the animal is able to swim by manipulating the cerata and rhinophores. This was mentioned by FARMER (1970) in his paper on swimming gastropods. However, it is doubtful that he has actually seen it swim and he is merely quoting what was stated by Risbec.

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Cypraea goodallii Sowerby, 1832 on Fanning Island

BY

HUGH BRADNER

Scripps Institution of Oceanography La Jolla, California

SEVERAL *Cypraea goodallii* Sowerby, 1832 were collected and studied on Fanning Island during the summer and winter of 1977. Fanning, a small atoll, is one of the Line Islands about 1 600 km due S of Hawaii and is one of the most easterly of the Pacific equatorial islands. There is only one deep-water pass into the lagoon.

Cypraea goodallii were collected throughout daylight hours at a rate of about one per hour in depths of 0.15 to 1.5 m under flat slabs of dead coral in calm water at the edge of the deep-water pass into the lagoon. The animals did not cling tightly and often fell off when the slab was turned. They were not associated with any particular sponge species.

Body and foot are cream colored. Foot is small. Mantle is almost transparent, with sparse 2- and 3-branched short white papillae. Siphon is short, white, with a ring of about 12 short stubble-papillae around the tip and along the underside. Antennae are orange-yellow, straight, gently tapered. Eyes are dark brown, small. One specimen was seen on a clump of about 100 eggs which have a color similar to that of the antennae.

Nematodes in the Alimentary Canal of Terrestrial Slugs

BY

DARIO T. CAPPUCCI, Jr.

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RELATIONS BETWEEN nematodes and mollusks have been reviewed by CHITWOOD & CHITWOOD (1937), MALEK & CHENG (1974), MENGERT (1953), PELSENEER (1928), STEPHENSON & KNUTSON (1966), and others. Based on known differences in life cycle patterns, nematodes may occur in snails and slugs (CHITWOOD & CHITWOOD, *op. cit.*; MALEK & CHENG, *op. cit.*) as follows: 1) normally free-living and plant parasitic nematodes that may pass through the host's digestive tract uninjured; 2) obligatory parasitic nematodes living in the host's digestive

tract; 3) nematodes with parasitic larvae occurring in the foot muscles of the host and with a free-living adult stage; 4) adult nematodes living in the genital organs of the host; 5) agamic nematodes that live in the body spaces of the host and that leave the host upon reaching maturity to lead a free-living existence; and 6) parasitic nematodes of vertebrates, the larvae of which occur in snails and slugs. As noted by MALEK & CHENG (*op. cit.*), some nematodes cannot be fitted into any of the above categories at this time because of lack of information about their life cycles.

According to OGREN (1959a, 1959b), nematodes are only occasionally encountered in gastropods, and hence the present writer decided to present his findings. During the years January 1973 through January 1978, a total of 657 snails [*Helix aspersa* Müller, 1774] and 645 slugs [439 *Deroceras laeve* (Müller, 1774), 200 *D. reticulatum* (Müller, 1774), 5 *Limax maximus* Linnaeus, 1758, and 1 *Arion circumscriptus* Johnston, 1828] were collected from the same location, a semi-rural tract approximately 1.2 hectares in size, situated at the junction of the city limits between Martinez and Pleasant Hill in Contra Costa County, California. Nematodes were obtained from only 4 slugs (all *D. laeve*, collected 10 May 1975) out of the total of 1 302 gastropods examined. Three slugs yielded one nematode each in the alimentary canal. From the intestinal tract of the 4th slug, 3 nematodes were recovered. The nematodes, all females, were morphologically the same. A positive identification was not made, however, due to the lack of male specimens. Further material is needed. The 6 specimens have been deposited with the Diagnostic Service, Department of Entomological Sciences, University of California, Berkeley.

This report illustrates a basic problem of obtaining ample and appropriate specimens of roundworms from gastropods in order to make a satisfactory identification of the parasite or pseudoparasite. The problem is one that concerns both the malacologist and the parasitologist (TURNER & PINI, 1960). Too often, hundreds or even thousands of mollusks may be examined in vain by the parasitologist, while the unsuspecting malacologist may innocently discard parasitized animals, and with them the nematodes. The cooperation between the malacologist and the parasitologist is encouraged for the more efficient elucidation of both natural and experimental mollusk-nematode relationships.

ACKNOWLEDGMENTS

Thanks are extended to the late Mr. Allyn G. Smith, Mr. Barry Roth, Mr. Robert E. Jones, Dr. George M. Davis, Dr. George O. Poinar, Jr. and Dr. Ruth D. Turner.

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INTERNATIONAL CONFERENCE ON THE HISTORY
OF MUSEUMS AND COLLECTIONS IN NATURAL HISTORY
(April 1979)

The Society for the Bibliography of Natural History, together with the specialist professional Biology Curators Group and the Geological Curators Group, are sponsoring this Conference, to be held at the British Museum (Natural History), London on the 4th to 6th April, 1979.

The increasing importance of and interest in Museums and their holdings in the Natural Sciences and the present growth of studies into their history, indicated that the subject required an International Forum. The aim of this Conference is to bring together specialists in the various disciplines from throughout the world, historians of science, curators, librarians and bibliographers.

To achieve this, papers are invited upon a very wide range of subjects, which will be presented in the 4 sessions of the meeting. The range of topics includes: the history of individual public and private museums; studies of museums within a particular geographical area, time-span, or scientific discipline; the lives and activities of collectors of fossils, minerals, plants, or animals; studies of natural history libraries and book-collectors; the history of zoos and botanical gardens; the sale and dispersal of notable libraries and natural history collections; the documentation of museums and private collections; the relationship of bibliography to collecting; and the growth of museums and studies on collections resulting from expeditions and exploration. All papers submitted, whether read or not, will be considered for publication in a special volume.

In addition to the sessions of papers, exhibitions of natural history collections, books and manuscripts will be prepared in London museums and libraries. It is also intended to visit other institutions in the Home Counties on the 6th April.

For further information, please contact:

Mrs. J. A. Diment (Organising Secretary), Palaeontology Library, British Museum (Natural History), Cromwell Road, London SW7 5BD, United Kingdom.

W. S. M.

THE 1979 MEETING of the Western Society of Malacologists will be held jointly with the American Malacological Union in Corpus Christi, Texas, August 5 through August 11. Meetings will convene at La Quinta Royale, a beautiful new motor inn one block from the shoreline. Field trips, workshops, and symposia on Gulf of Mexico mollusks and Life-Histories of Mollusca are scheduled. A call for contributed papers, on these and any other malacological topics will be issued early in 1979. Information about the meeting is available from Mr. Barry Roth, President, W. S. M., Department of Geology, California Academy of Sciences, San Francisco, CA 94118.

At the 11th Annual Meeting of the Western Society of Malacologists, June 30, 1978, the following slate of officers was elected to serve during the fiscal year 1978/79:

President:	Barry Roth
First Vice-President:	Dr. Vida C. Kenk
Second Vice-President:	Carol C. Skoglund
Secretary:	William D. Pitt
Treasurer:	Carol C. Skoglund
Members-at-Large:	Michael G. Kellogg David R. Lindberg

Applications for membership should be sent to Mrs. Carol C. Skoglund, *Treasurer*, 3846 E. Highland Ave., Phoenix, AZ 85018. Dues: regular membership - \$7.50; additional family members - \$1.00 per person; student membership - \$3.00. Regular and student members receive the Annual Report, containing the published proceedings of the Annual Meeting.

Back issues of many Annual Reports, and W. S. M. Occasional Paper No. 2, "A Catalogue of Collations of Works of Malacological Importance" by George E. Radwin and Eugene V. Coan, are available. Address requests to Mrs. Carol C. Skoglund, *Treasurer*, 3846 E. Highland Avenue, Phoenix, AZ 85018.

Sale of C. M. S. Publications:

Effective January 1, 1978, all back volumes still in print, both paper-covered and cloth-bound, will be available only from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA (lifornia) 93644, at the prices indicated in our Notes and News section, plus postage and, where applicable, California State Sales Tax. The same will apply to the Supplements that are still in print, except for supplements to vol. 7 (Glossary) and 15 (Ovulidae), which are sold by The Shell Cabinet, P. O. Box 29, Falls Church, VI (rginia) 22046; and supplement to volume 18 (Chitons) which is available from Hopkins Marine Station, Pacific Grove, CA (lifornia) 93950.

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[Part 1: Opisthobranch Mollusks of California
by Prof. Ernst Marcus;

Part 2: The Anaspeidea of California by Prof. R. Beeman,
and The Thecosomata and Gymnosomata of the Cali-
fornia Current by Prof. John A. McGowan]

[The two parts are available separately at \$3.- each]

Supplement to Volume 6: out of print.

Supplement to Volume 7: available again; see announce-
ment elsewhere in this issue.

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[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Volume 14: \$6.-.

[The Northwest American Tellinidae by Dr. E. V. Coan]

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A Glossary of A Thousand-and-One Terms
Used in Conchology

by WINIFRED H. ARNOLD

originally published as a supplement to volume 7 of the Veliger has been reprinted and is now available from The Shell Cabinet, Post Office Box 29, Falls Church, Virginia 22046, U. S. A. The cost is US\$ 3.50 postpaid if remittance is sent with the order.

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[A systematic Revision of the Recent Cypraeid Family
Ovulidae by CRAWFORD NEILL CATE]

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sion of Some Sessile Marine Invertebrates in Monterey
Harbor by Dr. E. C. Haderlie]

Supplement to Volume 17: Our stock of this supplement is exhausted. Copies may be obtained by applying to Dr. E. C. Haderlie, U. S. Naval Post-Graduate School, Monterey, CA (lifornia) 93940.

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[The Biology of Chitons by Robin Burnett *et al.*].

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Supplements

Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

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but before March 15 of the following year, there will be a re-instatement fee of \$1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of \$5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is \$25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

REGARDING POSTAL SERVICE

Complaints regarding late arrival of our journal are increasing in number, steadily, continually. However, we very conscientiously dispatch our journal on the printed publication dates. What happens after deposition at the Post Office is, of course, beyond our control. From some of our members we have been able to construct a sort of probable delivery schedule. In general, within California, 8 days is usual; outside of California, the time lapse increases with the distance; the East Coast can consider a lapse of "only" two weeks as rapid service; 4 to 5 weeks are not uncommon. Foreign countries may count on a minimum of one month, six weeks being the more usual time requirement and over two months not rare!

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address).

The Latest New Postage Rates

Effective on May 29, 1978, the U. S. Postal Service increased rates for first, third and fourth class matter, as announced some months before. However, although not announced publicly and without notification to publishers, second class postage rates within the United States were also increased. Further, again without advance notification, postage for second class matter to the so-called PU-AS countries (Spanish-speaking countries and Brasil), which had traditionally been lower than to all other foreign countries, was increased to the same rate.

On July 6 a further increase of postage rates within the United States went into effect. This increase came also as a surprise to us, since we had assumed that the May increase was taking the place of the so-called phased increases which are scheduled for the sixth of July each year.

It is obvious that we are forced to pass these increases on to our members and subscribers. Therefore, effective immediately, we must charge US\$3.50 for postage to all addresses outside the United States. What increases we may have to make in the U. S. A. remains to be seen.

As on several previous occasions, we are again the losers in this case. Since our subscription renewals as well as membership dues were due prior to the 29th of May, no provision for the increases had been made; and it is too costly to send out bills for the additional \$1.-.

The "phased" increases are, of course, acceptable since these are known to the publishers; but these unannounced increases may quite easily lead to the demise of many periodical publications. Frankly, we are very pessimistic about the future fate of our publication, not only because of these erratic increases in postage rates, but also because of the continued lack of improvement in the postal service. As our members are aware, we have already been forced to suspend publication of our supplements.

In this connection it seems desirable to once again stress the importance that changes of address (accom-

panied by the fee of US\$ 1.00) be communicated to us

AT LEAST SIX WEEKS

before our regular mailing dates. We must make an address change even if only one digit in the ZIP code is changed; the cost to us is the same as for a completely new address.

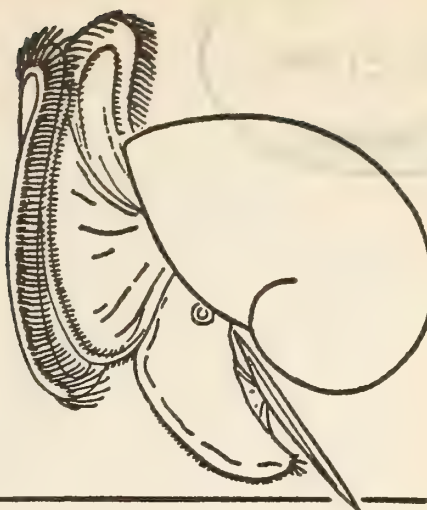
The Postal Service policy in regard to forwarding mail is generally not well known. First class matter will be forwarded up to one year if a request to that effect is filed. Second class matter will not be forwarded after 90 days, even if forwarding postage is guaranteed. Items that are not forwardable will be returned to the sender IF return postage is guaranteed. Since our copies frequently weigh in excess of one pound, return postage is very high. We have, in the past, had to pay as high as \$1.80 for returned copies. It is more than likely that return postage henceforth will also be higher. It should not surprise any person to realize that we cannot re-mail a returned copy without re-imbursement for return postage, postage incurred in correspondence with the addressee and the costs of re-packing and re-mailing. If prompt reimbursement is not made, we are forced to suspend service on the particular subscription or membership.

Under no circumstances are we able to supply free replacement copies of issues that fail to reach their proper destination. However, we will ship by insured mail replacement copies at half the announced single copy rate of the particular issue plus postage. We have developed a triple check system so that, if we say that a copy has been mailed, we are absolutely certain that we delivered that copy to the post office in Berkeley and on the date we indicate. From our experience with the loss of insured mail, we are tempted to suggest that subscribers figure on a 10% reserve fund for the purchase of replacement copies. The only alternative remaining would be for us to increase subscription rates and membership dues by at least 10%. This, however, does not seem quite fair to us as some of our subscribers in almost 20 years have never failed to receive their copies.

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THE VELIGER

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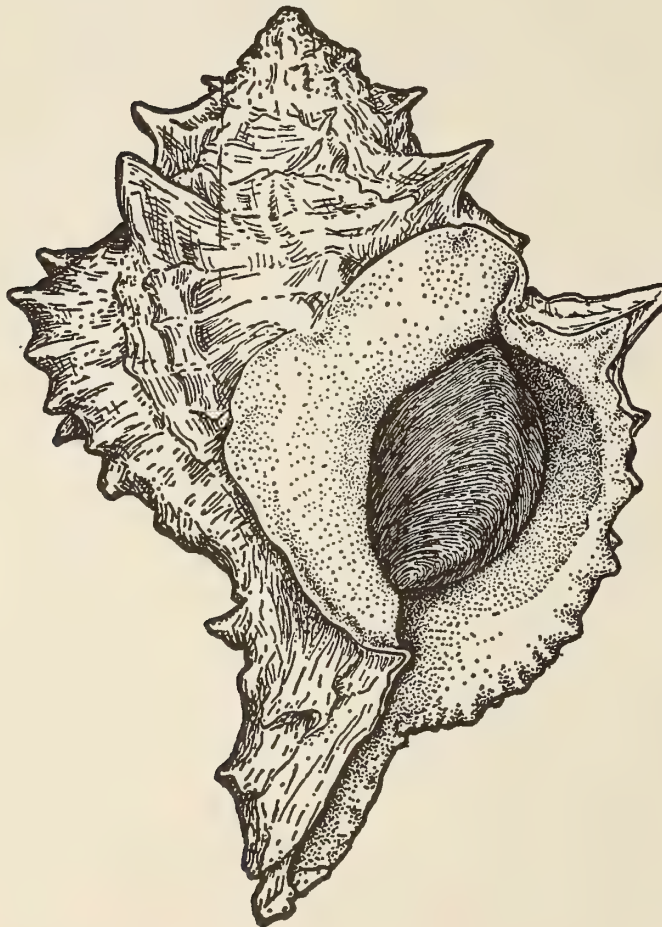
[Continued on Inside Front Cover]

Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus*, (*Subgenus*)
New Taxa

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A Comparative Study of the Structure, Development and Morphological Relationships of Chambered Cephalopod Shells

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(6 Plates; 27 Text figures)

INTRODUCTION

AMONG THE RECENT CEPHALOPODS, chambered shells are confined to the members of three families: the Nautilidae, with only a few species of *Nautilus* that represent the nearly extinct subclass Nautiloidea; in the Coleoidea (order Sepioidea) the monotypic Spirulidae and the speciose Sepiidae, the common cuttlefishes.

The shell of *Nautilus* is external, whereas the *Spirula* shell and the "cuttlebone" of the Sepiidae are internal, as are those of all coleoid cephalopods. The general aspect of these three types of chambered shell is rather different. The shells of *Nautilus* and *Spirula* show some resemblance in that they are coiled and have large chambers, in contrast to the cuttlebone which is straight and has numerous extremely narrow chambers. However, the coiling of the external shell of *Nautilus* is exogastric, whereas the coiling of the internal *Spirula* shell is endogastric. Despite its straight form, the cuttlebone presents signs of a close relationship with the coiled *Spirula* shell.

These general aspects were known in the last century. If there has never been a doubt about the buoyancy function of the gas-filled chambered shell, its actual functioning has only recently been elucidated. With the use of scanning electron microscopes, it has become possible to analyse in great detail the ultrastructure of these aragonitic shells, recent and fossil. This structural analysis provides a sound basis for the comparative study of the functional morphology of the chambered cephalopod shells, and

more particularly of their siphuncular system, which is known to be responsible for buoyancy regulation.

The present study follows this line of investigation. Along with the presentation of new data on the ultrastructure of the *Spirula* shell and of the cuttlebone throughout its development, a comparative account of the structural aspects of chambered shells in general is attempted, with the aim to unravel some of the complications arising from the different interpretations presented in the literature.

MATERIAL AND METHODS

Specimens of *Sepia* were collected at Banyuls-sur-Mer, (Western Mediterranean), Port Sudan and Suakin (Red Sea); *Spirula* shells on the Canary Islands (Eastern Atlantic) and at Santa Marta (Caribbean).

Shell material was prepared for observation in the Scanning Electron Microscope ("Cambridge Instruments") by oriented breaking, washing with distilled water (no etching!), mounting on metal supports and coating with carbon and gold.

Embryonic shells were removed mechanically and washed in water. For histological investigations, specimens were either fixed in Bouin's fixative, embedded in paraffin, sectioned at a thickness of 7 μ m and stained with Azan or Masson's Trichrome; or pieces of fresh material were fixed in 1% OsO₄ in sea water for 1 to 2 hours,

embedded in Epon, and sections ranging from about 0.5 to 1.5 μm were cut with glass knives on an ultramicrotome. These sections were stained with a mixture of Methylene blue and Azur blue.

CHAMBERED SHELLS IN SEPIOIDEA

Morphology and Structure of the Shell in *Sepia*

The shell of *Sepia* has been described in detail by APPELLÖF (1893). This author also discussed older literature dating back to the 18th century. The terminology we use for the different parts of the cuttlebone is largely adopted from Appellöf and translated from German (Figure 1). For some details, the terms used by DENTON & GILPIN-BROWN (1961), are given preference to those of Appellöf.

The cuttlebone consists of a dorsal shield ("Rückenschild") and the ventral chamber zone ("Wulst"). The spine ("Dorn", "Rostrum") is situated on the mid-dorsal line on the convex dorsal shield, close to its posterior end. The upper side of the dorsal shield is covered by calcareous tubercles; the posterior and the marginal portions are smooth. Appellöf called the part that surrounds the spine "Dornhülle," i. e., cover of the spine.

The ventral side of the dorsal shield bears the convex chamber complex, which thins out towards the posterior end. On the ventral surface of the chamber zone, we distinguish the siphuncular zone ("gestreifter Wulst") from the zone of the last-formed chamber ("ungestreifter Wulst"). The posterior portion of the chamber zone is embraced by the fork ("Gabel"). The fork is broad posteriorly and narrows anteriorly on each side; it ends near the siphuncular surface of the last-formed chamber (last "Wulststreifen"). A calcified rim ("verkalkte Randzone"), accompanied by an uncalcified outer rim ("unverkalkte Randzone") of the dorsal shield, surrounds the fork and the chamber zone.

The dorsal shield consists of three layers (Figure 2). These are the uppermost, dorsal layer ("Rückenplatte"), the central layer ("Mittelplatte") and the inner layer ("Innenplatte"). The central layer emerges at the rim of the dorsal shield; it is characterized by organic and mineralized lamellae. The inner layer begins somewhat inward of the mainly organic rim of the dorsal shield; it consists of two portions, an upper, coarsely columnar prismatic layer ("Pfeiler-", i. e., pillar-like crystals) next to the central layer, and a lower, spherulitic prismatic layer ("besenartige," i. e., broom-like crystals). The dorsal layer covers the upper intra-marginal portion of the dorsal shield. Appellöf differentiates between two portions, the middle and anterior undulating, nodular layer ("Höckerpartie") and the posterior area of the spine cover (cf.

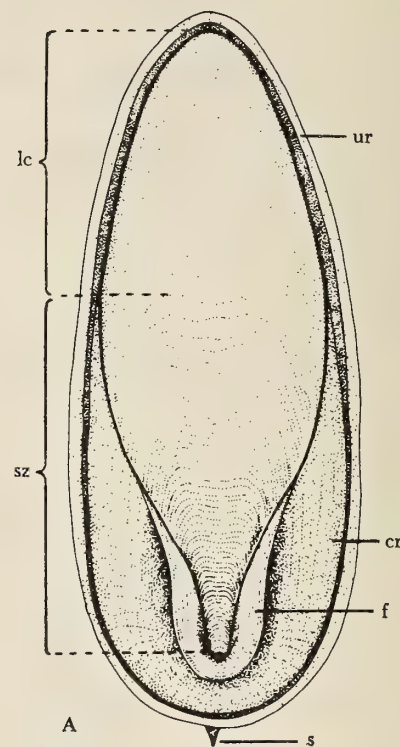


Figure 1

A:
Ventral view of a *Sepia* shell with the siphuncular zone (sz) and the last chamber (lc) surrounded by a calcified rim (cr) and an outer uncalcified rim (ur). The so-called fork (f) is restricted to the posterior part of the shell around the siphuncular zone. The spine (s), which projects from the dorsal side, is only partly seen at the posterior end of the shell.



B:
The position of the cuttlebone in the dorsal part of the mantle is shown in a swimming animal (cf. also Figures 10, 11, 15, 17, 98 and 99)

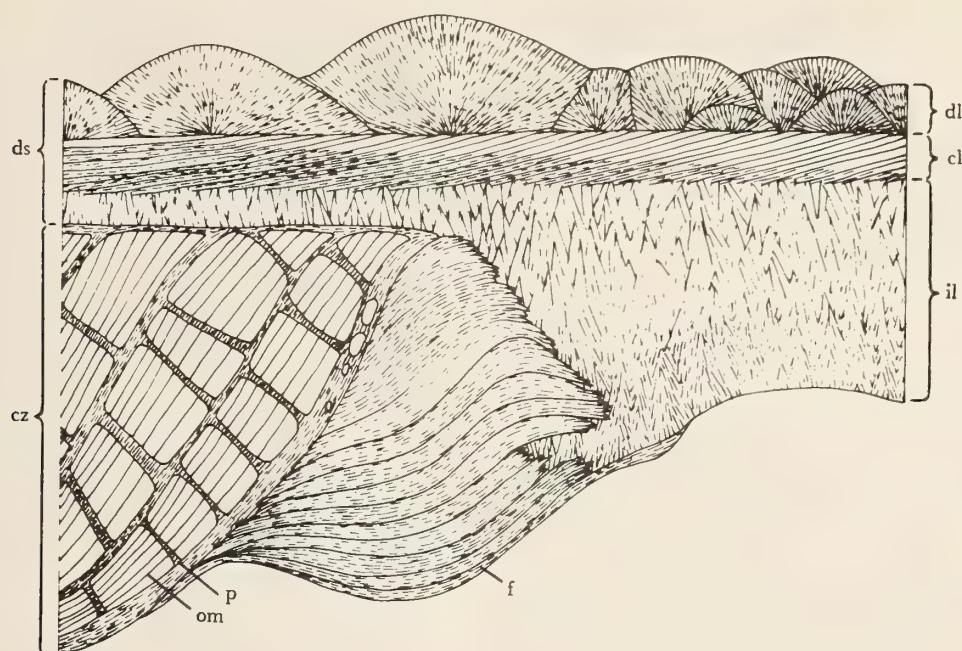


Figure 2

A cross section through the posterior part of the *Sepia* shell, showing the insertion of the chamber zone (cz) on the lower side of the dorsal shield (ds), the latter comprising 3 layers: the dorsal layer (dl), the central layer (cl), and the inner layer (il). Between the

marginal part of the inner layer and the chamber zone lies the fork (f). Within the chambers, organic membranes (om) are suspended between the pillars (p).

above). In our study, the spine and its surroundings are included in the central layer because of their structural similarity. The fork consists of several separate layers ("Gabelsepta"), each of which shows a finely laminated structure.

The chambered part consists of cavities ("Höhlenschichten"), separated by septa. Each septum is made of a chamber roof (ventral portion of the septum) and a chamber floor (dorsal portion of the septum) (Figure 3). Within the chambers, vertical pillars and walls ("Pfeiler") form the supporting elements of the septa. In addition to the septa, organic membranes are suspended between the pillars ("freigespannte Membranen") (Figure 2).

After a chamber is completed by the formation of the (ventral) chamber floor, formation of a new chamber starts with the chamber roof completing the last septum (cf. Figure 3). The chamber roof consists of a prismatic layer composed of rectangular, rod-like prisms ($0.4 \mu\text{m}$ wide) (Figures 28, 82). The smallest components which

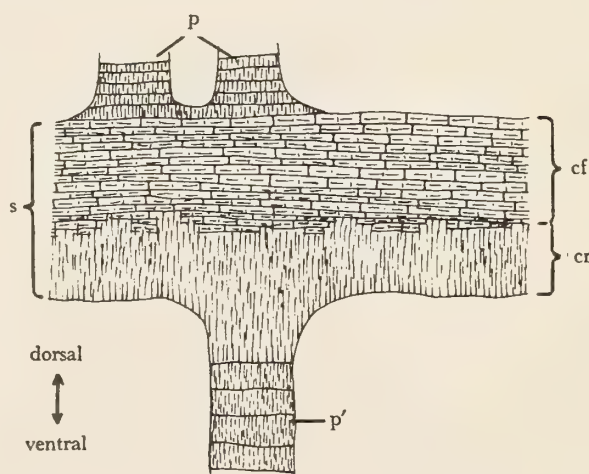


Figure 3

Cross-section through a septum of the *Sepia* shell. The septum (s) comprises the chamber floor (cf) with the base of the pillars (p) of the upper chamber and the chamber roof (cr) with the "tops" of the pillars (p') of the lower chamber

make up these prisms are angular elements with a width of $0.2\text{ }\mu\text{m}$. At the insertion of the pillars and pillar walls, the prismatic crystal rods of the roof extend, without interruption, into the base of the forming pillar. The chamber roof is about $7\text{ }\mu\text{m}$ thick; it is continuous with the floor of the older (upper) chamber (cf. below); there are no separating structures such as organic layers.

Where they emerge from the chamber roof, the pillars are either round, columnar, or they are straight or slightly undulating wall-like structures; these walls have about the same thickness as the columnar pillars. The prismatic structure of the chamber roof disappears in the basal part of the pillar; it grades into the lamellar structure with the appearance of the first annulation. The pillar annulations (38 to 62 in the central area of the chamber zone of *Sepia orbignyana*) are continuous in many pillars of one and the same area of a chamber, but they are not so in all pillars of a chamber. This can also be noted with the organic sheets that are extended between pillars. The central zone of one chamber may have 5 to 9 such sheets, extended parallel to the septa (Figures 29, 30). These sheets are not seen as distinct organic layers within the pillars, but probably they are continuous. Within the pillars, the organic material is incorporated in the crystal fabric. The organic sheets are often found to split into a number of thinner sheets when they approach a pillar, so that only thin organic sheets are incorporated into adjacent portions of the calcareous fabric of the pillar. The "fusion" of these thin sheets at some distance from the pillars is probably secondary; it may result from artifactual agglutination of the wet membranes during drying of the cuttle-bone.

The pillar annulations are $1\text{ }\mu\text{m}$ to $8\text{ }\mu\text{m}$ wide. The crystals making up the pillar lamellae are quite irregular in shape; the most common form is a brick-like component ($0.2\text{ }\mu\text{m}$ wide) with its long axis usually following the axis of the pillar (Figures 78, 79, 82).

Close to the chamber floor, the walls show stronger bending, and pillars tend to branch (Figures 30, 31, 80, 81). The surface of the pillars in the ventral part of the chamber is thus enlarged. Also wall-like pillars tend to divide into many branches, and columnar pillars show bilateral flattening in their different branches. Along with this crenelation and flattening, the undulating sheets thus "disintegrate". The ventral side of each chamber is therefore more permeable than the dorsal part, where the base of a pillar wall is generally continuous.

The crystal growth of the ventral pillar branches that turn into the chamber floor is continuous, without any organic or mineral layer between pillar and floor. KÄELIN's (1967) statement that the wall-like pillars are not solidly fused with the chamber floor is erroneous.

The chamber floor is about $15\text{ }\mu\text{m}$ thick; it shows a lamellar structure, with lamellae that are about $0.1\text{ }\mu\text{m}$ thick (Figures 28, 82). In its middle part, this floor layer is made of $0.2\text{ }\mu\text{m}$ wide, needle-shaped crystallites that show a common orientation within each layer. In their first-formed layers, the lamellar structure of the floor is composed of shorter rod-like elements, oriented parallel to the plane of lamellation. With its gradual transition into the roof of the next chamber, the lamellae show rod-like components with gradually changing orientation, from parallel to lamellation through vertical position, until lamellation is largely or entirely lost in the roof of the next chamber (Figure 28).

Away from the central region of the chamber, pillars become shorter (Figures 75, 76); in the anterior region of the chamber, they are fused into wall-like ridges or simple ridge-like structures. Towards the posterior end, close to the siphuncular zone of each chamber, the contrary is found. Here pillars become thinner and more columnar than in the central part of the chamber, and they are more closely set (Figure 31).

The number of organic sheets expanded between pillars decreases towards the anterior margin, where the chamber height decreases. This decrease is less distinct in the lateral parts, where the chamber height decreases more abruptly (Figure 2).

In the siphuncular zone, no calcareous floor is formed. The calcareous layers of the chamber floor are continuous with the organic sheets that cover the siphuncular area (Figure 31). In the siphuncular zone, the pillars are more numerous close to the posterior end of the chamber, where they are much shorter according to the lower chamber height. From the central area of the shell, organic sheets extend only in the foremost part of the siphuncular area. Here we find few sheets extended parallel to the roof; there are more sheets extended vertically between pillars (Figures 32, 33).

In the low posterior part of the siphuncular zone, between the short, thin pillars, we find a dense growth of short, columnar crystals, plate-like crystals, and crystal aggregates (Figures 34, 35, 36). These crystals are large in comparison with those forming the pillars, and they show well-developed crystallographic planes and faces (Figures 35, 36).

Near the posterior end of the chamber, the growth of crystals is so dense that they form a closure between the organic floor and the calcareous roof. Further anteriorly, the crystal growth forms a porous layer together with the rearmost short pillars. More anteriorly again, at about half of the length of the siphuncular zone, crystals may form aggregations of considerable height (Figure 36); between pillars, the first vertical organic sheets appear. Fi-

nally, in the foremost part of the siphuncular zone, the growth of distinct crystals comes to an end, and we find only columnar pillars sustaining the organic floor. This is the area where horizontal sheets are found between the pillars (cf. above). These sheets become more continuous above the rearmost part of the calcified chamber floor, and there the pillars take on a wall-like appearance.

The chamber height is approximately the same throughout the greater part of the chamber zone. Exceptions are the first chamber formed after hatching, which is often markedly lower, the zones of closely spaced chambers described by various authors (cf. BOLETZKY, 1974a), and the last chambers of the adult, senescent animal (Figure 30).

The formation of the dorsal layer begins rather late in embryonic development. In *Sepia officinalis*, it first appears in the form of an irregular crystal cover on the organic outer surface of the shell (Figure 37). In *Sepia pharaonis*, the first dorsal layer is made of nodular spherulitic structures (Figure 40). During further growth, the spherulite sectors start on the dorsal side of the organic central layer. The dorsal outer surface of the central layer is comparatively wide; the dorsal layer grows over it either by depositing directly ridge- or bump-like spherulitic structures that are surrounded by organic material (*Sepia elegans*, *S. pharaonis*), or with a zone of irregular fine crystal growth (*Sepia officinalis*, *S. orbignyana*). This may differ, however, among individuals as well as among different growth stages of an individual.

Towards the central part of the dorsal shield, the crystals are arranged in ridge-like aggregations, with a spherulitic orientation (Figure 38). Addition of crystalline material alternates with periods where organic material is added, but this periodicity seems not related to the formation of certain layers in other parts of the cuttlebone. Thus in a section or in a fraction, the dorsal layer shows varying sizes of crystal aggregates and different crystal diameters (Figure 44). Aggregates measuring 2 mm in diameter can be found on the adult cuttlebone of *Sepia officinalis*. Crystal diameters vary from 0.2 μm to 15 μm .

Near the spine or the structure corresponding to it (e.g., lamellar ridge in *Sepia elegans*), the dorsal layer is absent, as in *S. officinalis*, or it may surround the spine, as in *S. orbignyana*, or it is represented only by a very thin crystal cover of the ridge that represents the spine in *S. elegans*. In terms of its structure, the spine must be considered as part of the central layer (Figure 41), although it generally starts forming on the embryonic dorsal layers (Figure 39).

Finally, it should be mentioned that the structure of later deposits found on the posterior part of the siphuncular area consists of spherulitic-prismatic crystals and

thus can be compared to the dorsal layer (cf. below).

The central layer is the earliest to appear during embryonic development, where it is represented by the protoconch and the early organic shell. In the marginal parts of the shell that are formed later, it is also mostly organic; it is composed of sheet-like smooth organic layers that have been deposited in a succession directed towards the margins. The central layer is thin near the protoconch; it gradually thickens anteriorly, and more so towards the margins. Its lateral portion is always purely organic, whereas in the ventral part calcareous material is intercalated and interlocked with the organic sheets.

Since the organic sheets that are added to the margins of the dorsal shield are not continuous with others, but are deposited on sheets formed earlier, they form a low angle with the plane of the central layer (Figures 2, 46). At 9000 \times magnification, the organic sheets show no other substructure than a striation with a period of 0.1 to 0.2 μm .

Towards the inner layer, very thin and long lamellar crystal rods and long needle-shaped crystals may grow along with the organic sheets. Within a short distance, purely organic layers can turn into calcified layers (Figure 42). The calcified part of the central layer is much thicker above the chambers than near the margins (Figure 2). In the central part, the inner layer shows a lamellar structure. These lamellae form a low angle with the plane of the central layer, like the purely organic lamellae closer to the rim (Figures 2, 46, 47). Lamellae are ca. 1 μm in thickness; they are continuous throughout the extent that we have been able to follow. They do not branch, but they change in thickness when turning into the purely organic zone (Figure 46). They also show some variation in their thickness close to the base of the inner layer where they end. Lamellation largely or entirely disappears where the base of the coarse prisms of the inner layer appears (Figure 47).

Each lamella of the central layer is composed of rod-like elements which usually are identically oriented within one layer (Figures 48, 51). Among different lamellae, this direction may change. Sometimes the needle-like crystallites that compose the lamellae show a feather-like arrangement (Figure 49), are gently curved (Figure 50) or branched (Figure 48). No distinct organic sheets appear between lamellae, but organic and mineral (needle-like) shell material is interlocked with one another, thus forming one complex shell deposit of organic and mineral components. The construction of the lamellae in the central layer thus is similar to the construction of the lamellae in the septa and the fork layers.

These strongly calcified parts of the central layer that are continuous in the ventral portion of the dorsal shield above the chamber zone extend, in some species of *Sepia*,

onto the outer side of the dorsal shield where they build the spine and its surroundings. In *S. elegans* there is no distinct spine, but only a ridge made of organic lamellae, which are often covered by crystal aggregates of the outer layer. Sheets similar to those of the margins of the dorsal shield alternate with deposits of the dorsal layer.

The shells of *Sepia orbignyana* and *S. pharaonis* have strongly calcified, solid spines (Figure 84). These consist of layers very similar to those of the inner calcified portion of the central layer. From the margins towards the center of the spine, lamellae become continuously thicker and show an increasing amount of calcareous material. Thus the spine is made of cone-shaped layers that are piled up on one another. Each of these cone layers, which are thickest in their center, is continuous with a purely organic layer at the sides of the spine (Figures 41, 85). The actual spine is a purely lamellar structure, whereas in its surroundings the organic layers corresponding to the spine layers often are covered by materi-

al of the dorsal layer so that they interdigitate with the latter (Figure 14).

The structural features of the spine of *Sepia officinalis* are intermediate between those of *S. elegans* and *S. orbignyana*. In *S. officinalis*, the change from purely organic sheets of the central layer into the lamellar calcified layers of the spine is very abrupt (Figure 41). Thick organic sheets forming the margin of the posterior dorsal shield split into single sheets that connect the shield and the spine. Close to the spine, these layers again split into numerous free sheets, each of which is continuous with one lamella of the calcareous spine. In *S. officinalis*, the region around the spine is covered with organic sheets, which may or may not show minor growth of crystals having the structure of those that build the neighboring dorsal layer.

Certainly the layers that form the calcified spine in *Sepia* are part of the dorsal portion of the central layer; in other parts, e. g., in the marginal rim of the dorsal

Explanation of Figures 28 to 43

Figure 28: Fracture through septum of the chamber zone of *Sepia orbignyana*, showing a pillar rooted on the prismatic chamber floor (lower, ventral side of septum). The chamber floor is composed of the lamellar structure

× 1 400

Figure 29: Transverse section through the chamber zone of *Sepia gibba* showing narrow chambers separated by septa which are held apart by pillars. Suspended between the pillars in the chambers are organic sheets. The upper margin of the figure is ventral

× 28

Figure 30: Transverse fracture through the chamber zone of *Sepia orbignyana* showing the last formed chamber of an adult individual with decreasing chamber height. Note the organic sheets which are suspended within the chamber cavities between the pillars. The upper margin of the figure is ventral

× 180

Figure 31: Section through chambers of *Sepia orbignyana* in the siphuncular zone. Note in the lower chamber mostly round pillars close to the posterior end of this chamber. The upper chamber shows the anterior siphuncular area with short pillars. Above it the extreme posterior end of the siphuncular zone of the next chamber is visible, with irregular crystal growth and very short pillars. The siphuncular membrane is torn off and only its posterior portion is visible at the right. The upper margin of the figure is ventral

× 126

Figure 32: The siphuncular zone of a chamber of the embryonic shell of *Sepia pharaonis* during growth demonstrates the change of orientation of organic sheets from parallel to septa to vertical to septa. Also pillars become shorter and more numerous within the siphuncular zone

× 190

Figure 33: This detail of Figure 32 demonstrates the change in orientation of the organic sheets within the chamber in the siphuncular zone

× 430

Figure 34: The posterior end of the siphuncular area of a chamber of the cuttlebone of *Sepia pharaonis*, showing the organic siphuncu-

lar membrane (in the lower left), and where it is torn off the siphuncular zone of the chamber below it

× 380

Figure 35: This detail of Figure 34 shows the crystals of the posterior portion of the siphuncular zone with well-developed crystal faces

× 8 000

Figure 36: Another detail of Figure 34, with aggregations of crystals forming pillar-like structures that lie between short pillars in the central region of the siphuncular zone

× 4 000

Figure 37: The first irregular crystal cover on the organic, outer (dorsal) shell surface in the embryo of *Sepia officinalis*

× 3 700

Figure 38: A fracture through the central portion of the dorsal shield of *Sepia orbignyana* showing the lamellar central layer (lower part of figure) and the spherulitic dorsal layer. The latter forms ridges and crests on the dorsal side of the cuttlebone

× 420

Figure 39: Crystal growth on the posterior portion of the embryonic shell of *Sepia officinalis* at first is spherulitic, like that of the dorsal layer. Only later is it changed into the lamellar structure forming the spine at this location

× 1 600

Figure 40: The dorsal layer in the posterior rim of the dorsal shield of the shell with 6 chambers in young of *Sepia pharaonis* consists of isolated spherical structures

× 370

Figure 41: A detail of Figure 85 of the spine of *Sepia officinalis* demonstrates the rapid transition from organic sheets of the spine cover into the lamellar, calcified structure of the spine. The thick organic sheets split into thin lamellae near the calcified spine

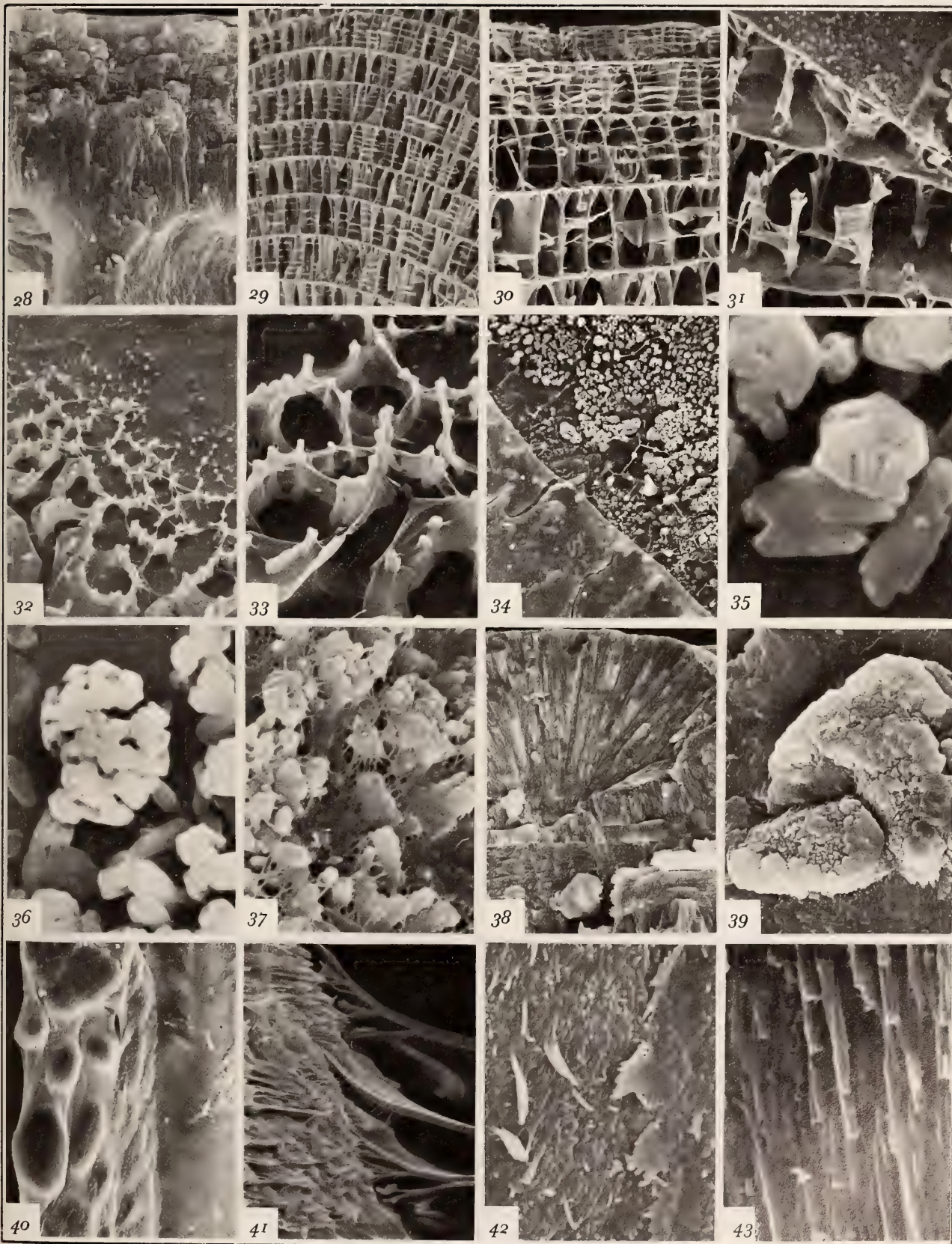
× 194

Figure 42: The central layer of *Sepia orbignyana*, broken parallel to the growth surface, shows the rapid transition from mineralized, lamellar structure to purely organic sheets

× 4 200

Figure 43: Crystal needles are present in the mainly organic deposits covering the posterior portion of the siphuncular area of the adult shell of *Sepia pharaonis*

× 3 900



shield and the area surrounding the spine, this central layer may be calcified to a much lesser extent or not at all.

On the ventral side of the shield, the inner layer comes very close to the margin; it overlaps the central layer. On the innermost organic sheets of the central layer, close to the prismatic base of the inner layer, there are more irregular needle lamellae. The needles merely show a general orientation according to a common direction; they are loosely spaced, so that there are interstices between them (Figures 49, 50). They may also be oriented in such a way that they form whorls that unite into columnar structures (Figure 50). In additional layers, closer to the base of the inner layer, such whorls turn into the round spherulitic nodules ($5\text{ }\mu\text{m}$ wide) that form the base of the prismatic inner layer (Figure 47).

The inner layer covers the ventral side of the dorsal shield from near the border of the uncalcified organic rim to the border of the fork layer (Figure 1). Only some of the innermost layers of the outer rim of the shield are calcified; they gradually turn into the inner spherulitic prismatic part of the inner layer, as shown above. The inner prismatic layer consists of coarse prisms that have an irregular outline (Figures 46, 47). In a section parallel to the growth face, the prisms form an irregular network with a mesh width (diameter of prism) of about $5\text{ }\mu\text{m}$. When viewed from the growth face, near the inner rims of the dorsal shield, the growing inner, prismatic portion of the inner layer shows well developed crystal faces (Figure 52). The crystal needles are not arranged strictly vertical to the growth face; they may unite into columnar units of spherulite sectors (Figure 53).

Further inside the inner rim of the dorsal shield, crystal size decreases, and the even growth of crystal heads is changed into a more nodular growth of crystal bundles; the components show less distinct crystal faces (Figure 55). In section, one notes a spherulitic prismatic orientation of the needle crystallites, which are now much thinner. Columnar structures consisting of crystal needles inclined towards a central axis form this lower layer (Figure 53). This lowermost (ventral) layer is only found beside the chamber layers, not above them (Figure 2). Above the chambers, there is a coarsely prismatic to spherulitic prismatic layer; its thickness decreases towards the medial part of the dorsal shield. Thus an oblong, oval field in the medial part of the dorsal shield is devoid of an inner layer. This oval field, which is broader anteriorly, is "left out" when the inner layer is formed on either side of the chamber layer (*i. e.*, not on the anterior rim of the newly formed chambers) (Figure 1). Here the calcified central layer forms the basement for the anterior portion of newly formed chambers.

The borderline between the inner layer and the fork layer is sharp and usually is marked by a furrow (Figure 55). Sections through the contact region between the inner and the fork layer even show cavities; these are bridged by organic sheets indicating the course of growth lines (Figures 2, 54). The region of contact between the inner and the fork layer shows signs of alternating approach and retreat of these layers during the secretion of the cuttlebone (Figure 2).

The zone of transition from the inner layer towards the central layer shows a more gradual change, especially where the medial parts of the dorsal shield grade into the strongly calcified inner part of the central layer (Figures 46, 47). A gradual change between these layers is also found near the rim of the shield, but is restricted to the width of a few lamellae (Figure 50).

The fork layer is broadest and thickest in the posterior part of the dorsal shield. Its anterior ends often thin out before they reach the siphuncular area of the last-formed chamber; they may also extend beyond it. There does not seem to be a direct continuation of fork layers into chamber septa. Since the fork grows in length only anteriorly, its layers are piled up on one another. In adult *Sepia*, 12 to 15 such layers with a maximal thickness of $25\text{ }\mu\text{m}$ may be present on the ventral side of the cuttlebone. In their thickest part, these layers are made up of roughly 40 lamellae (Figure 59). These lamellae are composed of minute needle crystals ($0.3\text{ }\mu\text{m}$ in width), which are uniformly oriented within a lamella (Figure 56). Separation of thicker layers is due to the presence of more organic lamellae between the calcified ones that form the thicker layers (Figures 56, 59).

On the margins of the fork, each layer extends to a different degree onto the chamber zone, on the one side, and onto the inner layer, on the other side (Figure 2). A more strongly mineralized layer shows a growth front consisting of flattened rod-like needles that encroach, in the form of a sheet, upon the basement (Figure 58). There is only in some places a uniform orientation of the needles, as many lamellae grow at the same time, so that their fronts overlap one another. In mainly organic parts of the fork layer, the needle-like crystals are regularly arranged and maintained within organic sheets, where they are covered and surrounded by organic shell material (Figure 59).

In the posterior part of the siphuncular area, adult individuals of *Sepia officinalis* and *S. orbignyana* often show tubercular deposits that consist of aragonitic needles in a spherulitic prismatic orientation, like those found in the dorsal layer. Thus the siphuncular membrane of the oldest chambers, which are refilled with liquid, becomes impermeable.

In *Sepia pharaonis*, a crescent-shaped deposit consisting of a thick layer of mainly organic sheets is secreted on a very prominent tubercular deposit in the posterior part of the siphuncular area (Figure 4). Within these



Figure 4

Ventral view of the posterior part of the cuttlebone of *Sepia pharaonis*. The rear end of the siphuncular zone (belonging to the earliest chambers) is covered by a crescent-shaped deposit that consists of mainly organic layers with calcitic and aragonitic crystals.

sheets there are mineralized spots. This is the only case where calcitic crystals exist besides aragonitic ones in the shell of *Sepia*, as has been demonstrated by X-ray diffraction. The needle-shaped crystals are distributed in distinct spots of irregular outline; they lie parallel to the plane of the organic sheets and generally parallel to one another (Figure 43) (cf. also ADAM & REES, 1966: plt. 8).

It should finally be emphasized that the intricate system of organic sheets and threads interspersed with the calcareous structures is only partly chitinous. JEUNIAUX (1963) has analysed the shell of *Sepia officinalis* and found that 4.4% of the chambered zone is organic. Of this portion, only about $\frac{1}{4}$ is chitin. This author also indicates that the dorsal shield contains chitin (cf. also RUDALL & KENCHINGTON, 1973).

Morphology and Structure of the Shell in *Spirula*

The shell of *Spirula* was first described in detail by APPEL-LÖF (1893) and more recently by MUTVEI (1964a) and

DAUPHIN (1976). Scanning electron microscopy was used for the study of the septal layers by MUTVEI (1970), ERBEN (1974) and DAUPHIN (*op. cit.*). Our description is therefore largely restricted to features of the *Spirula* shell that were not described or mentioned in the earlier literature.

The initial chamber of the shell is almost spherical. It is only slightly higher (0.7 mm) than wide (0.5–0.7 mm). Nearly the entire wall consists of a single layer, since nodular deposits of the outer layer are sparse and are entirely restricted to the anterior dorsal side of the initial chamber. The wall of this chamber has a thickness of 10 μ m; it consists of a very regular prismatic layer (Figures 64, 66). The needle-shaped crystallites composing this layer are arranged parallel to each other and vertical to the inner and outer surfaces of the chamber. In the prismatic layer one can distinguish an outer and an inner part (not including the spherulitic-prismatic structure of the dorsal layer, which is added later). The outer layer is rich in organic material, whereas the inner layer shows fewer organic deposits. The surfaces of the inner and outer layer are devoid of any organic cover.

The apertural end of the first chamber is 0.38 mm wide; it shows a strong constriction which is much more pronounced than the constrictions between later chambers. The apertural lumen is taken up entirely by the siphuncular tube; the latter is inserted on the inner walls of the constriction and extends into the lumen of the chamber (Figures 64, 66). The end of the siphuncular tube is continuous with an organic sheet that is fixed to the opposite wall of the chamber (Figures 64, 65). Between the prismatic outer wall of the constriction and the insertion of the siphuncular tube lies a prismatic ridge (Figures 66, 73). The side of this ridge that slopes into the first chamber shows more organic material in its fabric than the opposite side. Crystallites are arranged vertically to the surface of the ridge. From inside the first chamber, this ridge appears as a low rim that surrounds the siphuncular tube, from which it is separated by a deep, narrow depression (Figure 64). From the constriction (aperture of the first chamber), the siphuncular tube decreases apically in diameter until it reaches its extended tubular end which is about 0.1 mm wide.

The pear-shaped siphuncular tube is inclined towards the ventral side of the chamber. The calcified portion extends into the chamber for about 0.3 mm. It is composed of lamellar layers in the structure of the septa that are formed later on (Figures 66, 73). This tube is generally closed by a hemispherical cap that is continuous with the organic sheet mentioned above. The longitudinal wrinkles of the sheet continue into wrinkles that cross the organic cap in a radial orientation (Figures 5, 65).

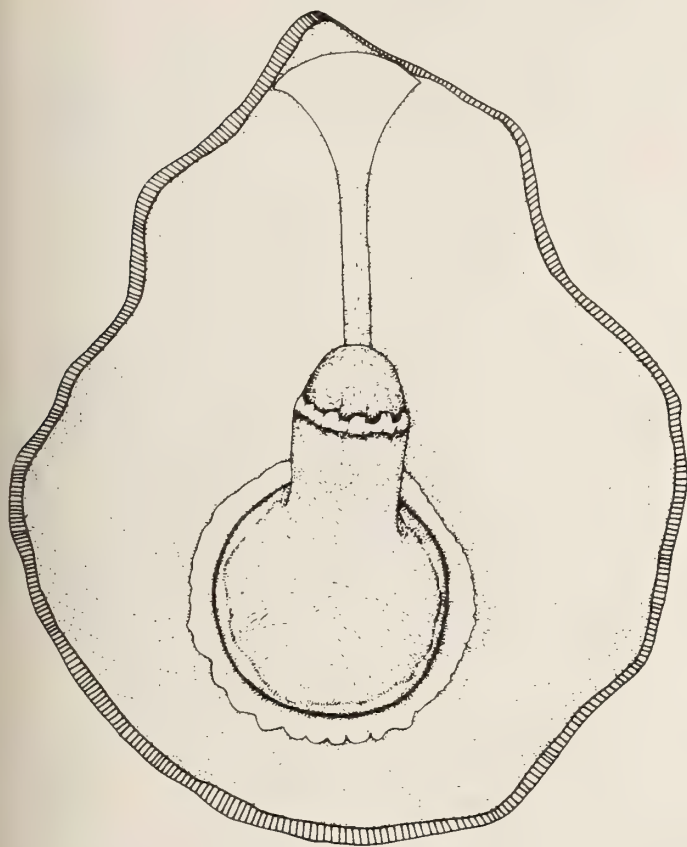


Figure 5

The first chamber of the *Spirula* shell opened up, exposing the earliest part of the siphuncular tube with its wrinkled surface, and its attachment to the inner wall via the organic sheet that is roughly spatulate. The site of attachment presumably marks the protoconch area

The organic cap may continue into the mineralized portion of the siphuncular tube without any break in its outline. But it may be altered in its structure when it has collapsed and the resulting shape has been fixed by the addition of organic material (Figure 87). More commonly, however, the diameter of the cap is slightly smaller than the diameter of the uppermost part of the calcareous tube, so that the transition from one structure to the other is marked by an edge (Figures 64, 66). The wrinkles mentioned before cross this edge and continue

in the outer organic cover of the calcareous siphuncular tube.

After the primary siphuncular tube of the first chamber (which is devoid of a septum) is completed, the normal growth of the shell begins with the formation of septa and the siphuncular tube. In contrast to later sections, however, in the second section of the siphuncular tube the pillar zone is extremely short (Figures 66, 68).

The outer wall of the *Spirula* shell consists of 3 layers, except for the first chamber (Figure 67). The outermost, dorsal layer may or may not be continuous on the dorsal side; it has a sculpture of nodular structures. On the ventral side, the dorsal layer is continuous; it consists of prismatic to spherulitic needle-like crystallites. The main portion of the shell wall is represented by the central layer (Figure 67). In polished sections viewed under the light microscope, it appears to consist of a prismatic structure with many parallel organic lamellae that cross the prisms, parallel to the inner and outer surfaces of the shell (cf. MUTVEI, 1964a: pls. 17, 18, fig. 2). In fractures, this layer shows a construction of small granular to brick-like crystallites that are not arranged in vertical needles; they present a slightly irregular arrangement in lamellae that lie parallel to the growth face (Figure 72). Single crystallites are about $0.4 \mu\text{m}$ long and $0.2 \mu\text{m}$ high; they are always enveloped by organic shell material. The construction of the central layer very much resembles

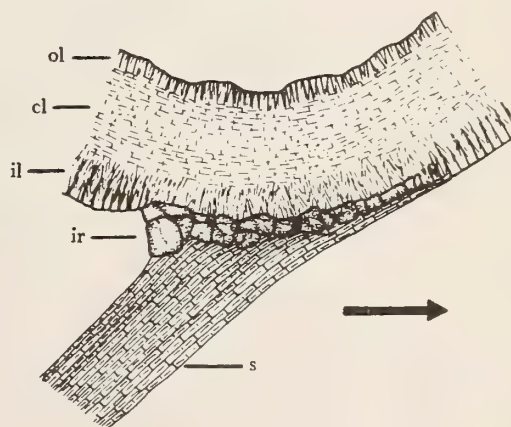


Figure 6

A longitudinal section through the outer wall of the *Spirula* shell, at the insertion of a septum (s) on the coarsely prismatic inner rim (ir). The outer shell wall consists of the outer, irregularly prismatic layer (ol), the central, lamellar layer (cl), and the inner, prismatic layer (il). The arrow points towards the aperture

that of the columnar siphuncular pillars (cf. below). The central layer forms more than half of the outer wall. It grades into an inner prismatic layer of somewhat variable thickness (Figure 67). This change is characterized by the arrangement of the crystallites in vertical needles of continuously increasing width towards the inner surface of the chamber. In tangential sections, these needles show up as a polygonal network (cf. MUTVEI, 1964a: plt. 18, fig. 2).

Where the septa are inserted on the outer wall of the shell, the inner layer shows a particularly coarse prismatic structure (Figure 6). It forms an inner rim that reinforces the constriction of the chamber aperture (Figure 88).

The septum consists of a lamellar needle layer. At the insertion on the outer wall, the inner side differs in its structure from the outer side. The inner side (facing the newly closed chamber) is marked by an abrupt ending of the lamellar needle layers (Figures 6; 88). They are inserted on the prismatic ring mentioned above, which is

similar to the additional constriction formed at the aperture of the first chamber (Figures 66, 73).

On the apertural side of the septum, lamellae extend further anteriorly, on the inner surface of the newly formed chamber ("living chamber") (Figure 6). The growth surfaces of the last-formed septal layers show a gradation from fine crystallites on the septum to coarse crystallites towards the inner prismatic layer of the wall that follows anteriorly. The outermost layer of the septum is lamellar, but the orientation and the composition of the needles are not as regular as in the layers next to it. The lamellae of the septum, from the first formed one to those lying under the last formed lamellae, consist of needle crystals that have a width of $0.2\ \mu\text{m}$ and show the same orientation within a lamella. The thickness of each lamella is given by the width of the single layer of needle crystallites and their organic cover. Although the orientation of crystals may change from one lamella to another, one sometimes finds series of lamellae in which the crystals

Explanation of Figures 44 to 59

Figure 44: A section through the dorsal layer of the cuttlebone of *Sepia orbignyana* showing the irregular spherulitic structure

× 335

Figure 45: A detail of Figure 74 showing the first mineral deposits on the dorsal side of the embryonic shell cap of *Sepia officinalis* that raise the contrast of radial sculpture and transversal growth lines

× 140

Figure 46: Section through the cuttlebone of *Sepia orbignyana* shows the transition from the lamellar structure of the calcified portion of the central layer to the columnar base of the prismatic inner layer

× 1 800

Figure 47: Detail of Figure 46 shows the rapid transition from the central layer (lower part of figure) to the inner layer

× 4 600

Figure 48: Calcified central layer of *Sepia officinalis*, broken nearly parallel to lamellation, demonstrates the composition by rod-like crystallites

× 4 700

Figure 49: A feather-like arrangement is present in the central layer of the *Sepia orbignyana* shell, broken parallel to the growth surface, near the outer side of the shield and close to the transition into the inner layer. The needles are loosely spaced

× 4 000

Figure 50: Crystallites of the central layer in almost the same position as in Figure 49, forming whorls that unite in columnar structures and form the base of the coarse prisms of the inner layer

× 4 000

Figure 51: The central layer of *Sepia officinalis*, broken nearly parallel to the lamellation, demonstrates its composition of small rod-like crystallites composed of small basal units of 0.1 to $0.2\ \mu\text{m}$ in size

× 5 000

Figure 52: Growth surface of the lower portion of the inner layer in the shell of *Sepia orbignyana*, near the inner rim of the dorsal shield, with well-developed faces

× 4 500

Figure 53: The inner layer of the cuttlebone of *Sepia orbignyana* showing below the dorsal coarse, prismatic portion and above the ventral finer, spherulitic-prismatic portion

× 930

Figure 54: A section through the fork layer (right) and the inner layer (left) of the shell of *Sepia orbignyana* shows the sharp border between both layers and cavities separating them, bridged only by organic sheets

× 270

Figure 55: The boundary between the inner layer (right) and the fork layer (left) in the shell of *Sepia orbignyana* is formed by a deep groove on the growth surface

× 880

Figure 56: The fork layer of *Sepia gibba* is composed of needle-like crystallites surrounded by and intergrown with organic material. Needles of each individual layer show the same orientation, but this orientation may differ among layers

× 4 500

Figure 57: Detail of Figure 84 shows the orientation of the first crystal growth near the spine of *Sepia pharaonis*, in an animal ready to hatch. Crystal needles have the same orientation within each aggregate, but are not yet oriented as regularly as within the lamellar structure of the spine itself

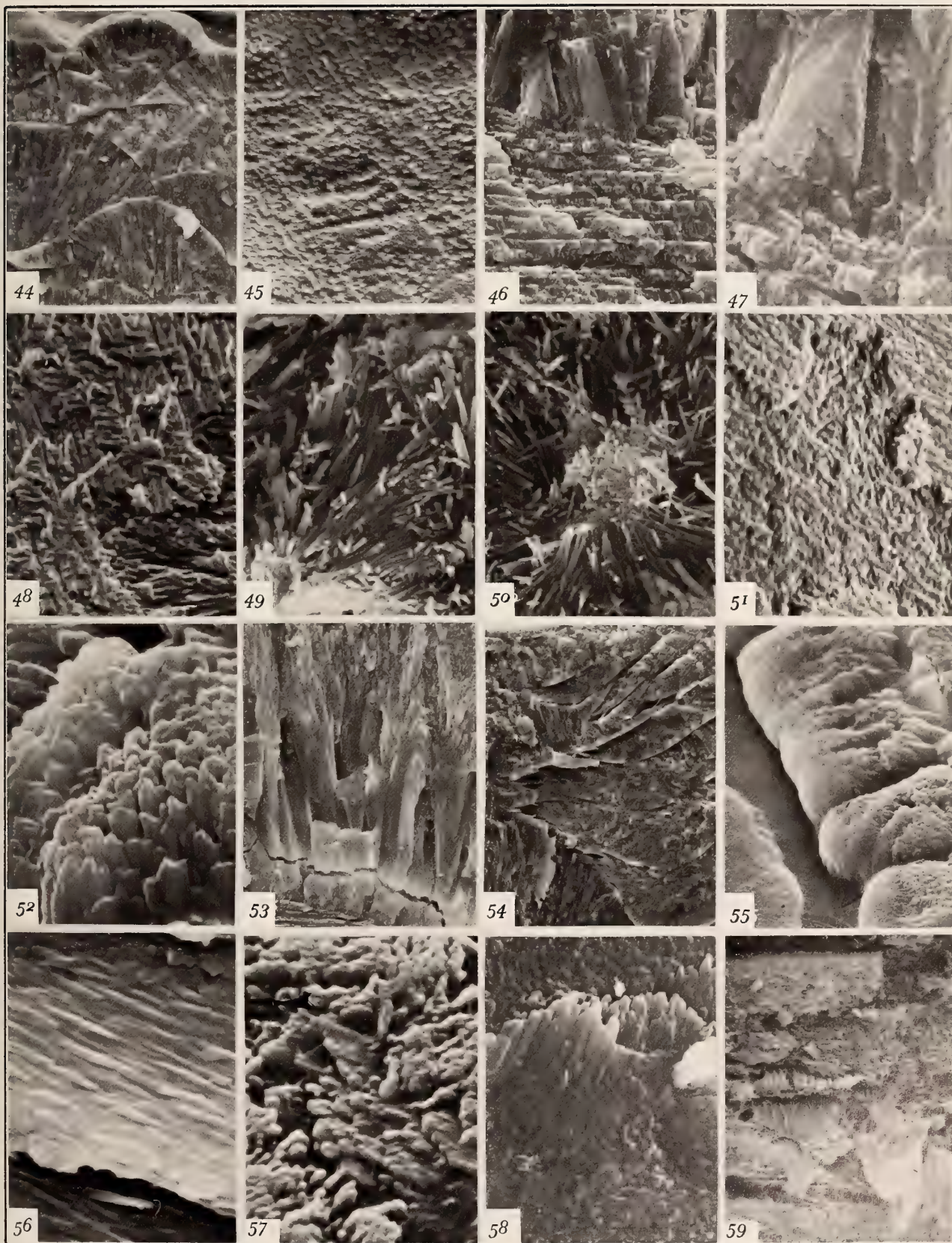
× 7 800

Figure 58: The growth surface on the central portion of the fork of *Sepia orbignyana* shows flattened, rod-like needles encroaching upon its surface

× 3 800

Figure 59: The fork layer of *Sepia officinalis* in a fracture shows the fine lamellation formed by $0.2\ \mu\text{m}$ thick layers composed of crystal needles and organic sheets. Some thicker organic sheets extend over the fracture and are hanging down from it

× 2 300



are all oriented identically. They are always well separated by organic material (Figure 62).

On the apertural surface of the septum, the lamellar crystal growth is more dendritic (Figure 60). Single lamellae tend to split into 2 lamellae by dendritic branching of crystal needles, with the thickness of needles remaining similar ($0.2\ \mu\text{m}$) to that observed in deeper layers. Towards the periphery of the septum (apertural side), needles and rods or prisms are oriented along 2 to several axes (Figure 61). The crystallites then become much wider and the crystalline faces become clearly visible. Further away from the septum, the size of crystals may remain unchanged, but lamellation completely disappears and is replaced by a vertical arrangement of needles. The orientation of growth increments on the crystal heads in 2 or several directions gradually disappears until a random pattern is established in the normal inner prismatic layer.

The layers of the septum are continuous with the si-

phuncular tube. The structure of the lamellar needle layer of the outer wall of the tube, which we find already in its blind end (Figure 66), continues through the chamber. Only below the septal neck of the following septum, the lamellar layer splits into 4 parts (Figure 7). The outermost layer is continuous with organic sheets. In newly formed, closed chambers, these organic sheets form a layer that closes the entrance to the space in which the pillars lie (Figure 69). These pillars are rooted on the inner side of the siphuncular tube, the foremost (apertural) ones being set on the concave surface of the septum where it turns into the septal neck. Their growth ends with the formation of the posterior part of a new siphuncular tube (Figures 68, 70).

Organic sheets extended between the pillars are found only in the apertural part of the pillar zone (Figure 7).

From the innermost lamellar layer of the last formed siphuncular tube, pillars always grow up without any

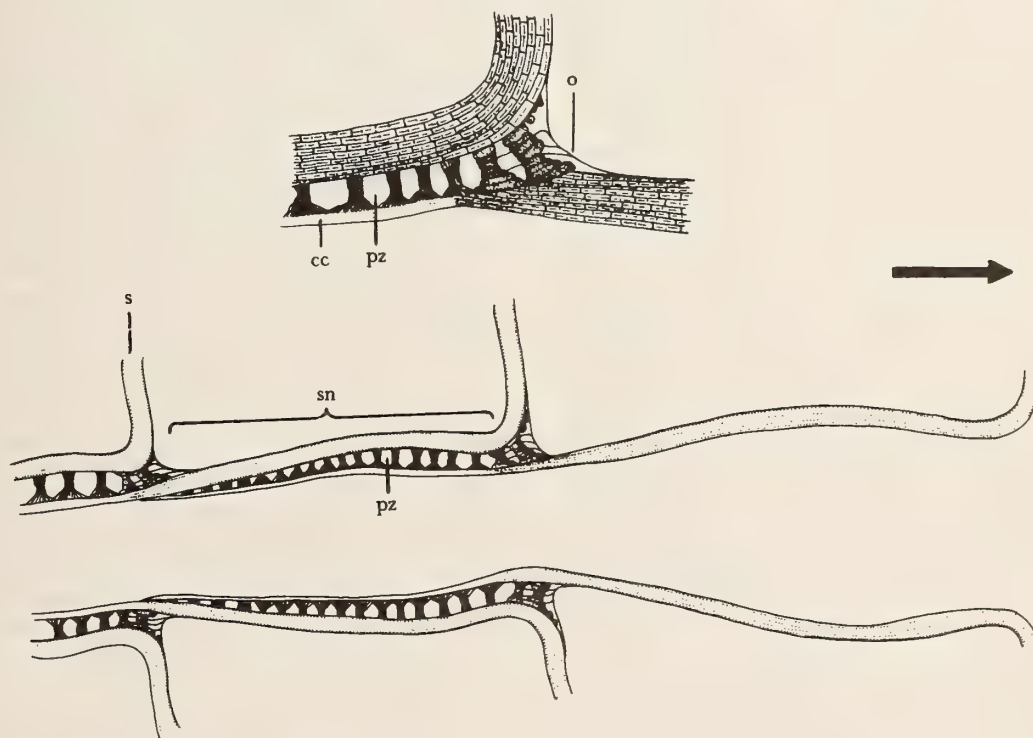


Figure 7

A horizontal section through the siphuncular tube of *Spirula*. The layers of the septum (s) continue into the siphuncular tube. At the entrance to the septal neck of the next older septum, the lamellar

layers split into organic sheets (o) that shut up the pillar zone (pz), organic sheets and pillars of the entrance, pillars of the middle pillar zone, and finally into the organic and crystal cover (cc) of the pillar zone. The arrow points towards the aperture.

separation by organic sheets. The shape of the pillars varies, however, according to their respective position along the siphuncular tube.

In the anterior zone, they form solid structures of bi-conical appearance with terrace-like annulations; they are broadly rooted on the bend of the septal neck and on the apertural part of the siphuncular tube (Figure 70). In front of complete pillars, small mounds and half-grown pillars with the typical annulations are found. The foremost complete pillars show only 10 to 15 annulations or growth zones, each of which is the continuation of one lamella of the anterior part of the tube. In this part, the lamellae may measure up to 15 μm in thickness. The free space between pillars is about equal to the diameter of these. On the inner siphuncular tube (the "floor"), the ends of the pillars fuse to form a solid, non-porous tube (in the anterior-most part of the pillar zone only!) (Figure 71).

Further inward, pillars have a more columnar shape and smooth surface, on which 50 to 60 lamellar layers can be counted (Figure 86). These are continuous with lamellae of the central part of the anterior siphuncular tube. Spaces between pillars are much wider than in the anterior pillar zone; they correspond to twice the diameter of a pillar. The lamellar structure of the base of columnar pillars is similar to the central layer of the outer shell wall. It consists of short needle- or brick-shaped crystals that are arranged vertically to the axis of the pillar (Figure 63). In contrast to the pillars of the anterior pillar zone, the pillar ends do not form a solid cover of the inner siphuncular tube. Instead, the radiating crystals and crystal aggregations form an interlocking system with many small spaces (Figure 71). In these, numerous thin organic sheets are transversally suspended. This porous layer of interlocking needle aggregations is covered by a smooth, thick organic sheet. The fourth (inner) section of the lamellar layer of the anterior tube is continuous with this uncalcified layer; it forms the innermost part of the shell that is in direct contact with the living tissue of the siphuncle. The transition from the calcified lamellae of the anterior tube to the organic inner layer is quite abrupt (Figure 7).

Further inward, towards the end of the inner tube, pillars are very short and drum-shaped; the interlocking crystal aggregations are growing into the spaces between the pillars.

A section through a double-walled siphuncular tube thus shows 4 layers: an outer lamellar layer, the pillars, the interlocking needle aggregations, and the inner organic layer. The anterior tube of the last septum shows a single wall that consists of the lamellar layer only. The 3 inner layers are added when the next septum is formed

(Figure 7). It should be noted here that the inner organic layer is destroyed by acids, whereas the organic components of the layers with lamellar structure are resistant.

The formation of a new septum and siphuncular tube section can be figured in the following way. First of all, the animal has to begin the outer wall of the new chamber (DENTON & GILPIN-BROWN, 1971). Then an annular prismatic ridge is formed at the border between the old and the new chamber, so that the constriction between them is reinforced. Meanwhile the tissue of the siphuncle must have grown to a sufficient density to be stretched over the length of one chamber. When the living tissue withdraws from the old chamber, it produces organic sheets that cover the wall left behind. When all the tissue has withdrawn, these organic sheets entirely cover the walls of the liquid-filled space. Now calcification begins, from the septal rim all through the septal neck into the siphuncular tube of the older chamber. The organic covers of the septum and the anterior siphuncular tube are integrated into the first lamellar layers, so that they can no longer be traced. As we have said above, free organic sheets will cover only the outer walls and the apertural side of the (old) septum and close the aperture between the anterior and posterior part of the siphuncular tube when the tissue withdraws from the "living chamber." Apparently the first lamellar layers deposited on the rear flanks of the prismatic ridge are secreted at the same time as the lamellar layers in the anterior part of the tube, the thick layers of the anterior pillar zone (with intercalated organic sheets), and the thin lamellae at the base of the pillars in the middle zone. The medial parts of the septum and the anterior tube form along with the upper portions of the anterior pillars that are fused into a calcareous ring, and with the upper portions of the medial pillars. The growth of the last septum layers is connected with the formation of the irregularly prismatic, porous layer and the first layers of the organic, soluble inner sheet. The septum is now completed, whereas in the siphuncular tube calcareous and organic lamellae continue to form at lower rates of growth until a new chamber is added. With the completion of the septum, the newly closed chamber can be used as a buoyancy element.

Development of the Shell Complex in *Sepia*

The early development of the shell complex in *Sepia* embryos has briefly been described by APPELLÖF (1893), and observations made by earlier authors are discussed there. A handicap of all these descriptions was the lack of a comprehensive staging system. The relation between morphogenetic processes and differentiation in different

parts of the embryo does not clearly show up, therefore. It was a great advance when NAEF (1923, 1928) introduced a good system of embryonic stages (stages I to XX). On his figures one can follow a great part of the complex morphogenetic processes by which an originally thin cap of embryonic tissue (the typical blastodisc of the telolecithal cephalopod egg) takes the form of a compact organism. In the center of this embryonic cap, the future shell epithelium can be made out at very early stages. It is surrounded by an annular thickening, which is the rudiment of the muscular mantle.

In all decapod cephalopods (cuttlefish and squids) so far studied, the subsequent process of the closure of the shell sac rudiment is essentially identical. First an annular ridge forms at the periphery of the mantle epithelium. This ridge then becomes a fold which grows centripetally over the mantle epithelium. The central opening of this mantle fold becomes slightly cornered, with one anterior (dorsal) and 2 lateral angles, before the shell sac is closed. The "scars" of the anterior and lateral angles will later differentiate into the so-called organ of Hoyle, which acts as a hatching gland.

As soon as the shell sac is closed, at stage XI of Naef, formation of the embryonic shell begins. The histological aspects and the general differentiation of the early mantle epithelium and of the closed shell sac have recently been described by SPIESS (1972). His description ends with stage XVI when histological differentiation is still in progress. Some complementary remarks must therefore be made for the later embryonic stages, and in some respects also for the earlier stages described by this author. The following brief description is based entirely on our own observations.

At the earliest stage of shell sac formation (stage VIII of Naef), the flat shell epithelium is characterized by roughly columnar cells, which are much higher in the anterior and middle parts of the epithelium as compared to the posterior part. The nuclei lie closer to the cell base, so that the apical parts of the cells together form a "plasma border"; the latter contains numerous vacuoles. In the middle and anterior parts of the epithelium, the nuclei of the closely packed cells lie at different levels, so that in these parts of the epithelium 2 or 3 layers of cells would seem to exist. However, there is no horizontal stratification of the cells. This primary shell epithelium is clearly separated from the underlying mesoderm.

The further development of the annular ridge, which already takes the shape of a fold by stage VIII, leads to the formation of the so-called "secondary shell-epithelium," which will be the "ceiling" of the shell sac. From histological sections, it appears that this lower (inner) cover of the closing fold is stretched during the closure

of the shell sac. Mitotic figures observed close to the opening show, however, that cell division continues also in this inner part of the fold. This means that the secondary shell epithelium forms *in situ* from ectodermic cells given off by the parts derived from the early annular ridge. This secondary shell epithelium remains thin, with its flattened nuclei widely separated. Its thickness gradually increases towards the periphery of the shell sac, *i. e.*, in the zone of transition to the primary epithelium.

By stage IX, the greater part of the primary shell epithelium is covered by the closing fold (the latter is filled with mesodermic cells that form a rather loose "mesenchyme"). Complete closure of the shell sac occurs between stages X and XI. The closing pore lies in the posterior part of the sac, about $\frac{1}{3}$ of its length from the posterior end.

The closure of the shell sac is coordinated with the general contraction of the embryo cap. The organ rudiments which had been lying in the single plane of the thin cap are now "assembled" in a three-dimensional arrangement, which largely corresponds to the definitive organisation of the animal. During these stages of assembly, the primary eye vesicles and the statocysts close, the stomodaeum is invaginated, and the funnel and mantle margins rise as distinct folds. The mantle complex thus takes its cup shape. The shell sac, which occupies the dorsal part of the mantle complex, remains comparatively flat, but its posterior and lateral parts are slightly bent to the ventral side.

The initial shell or protoconch, which is secreted immediately after closure of the shell sac, is roughly spoon-shaped, with its deepest part near the posterior end. It is a simple organic membrane, without any growth lines, about 0.9 mm long and 0.7 mm wide. During the following stages, organic material is added to the margins of this protoconch. The outline of the shell becomes ovoid. Along with the deposition of more organic shell material, the posterior slope of the embryonic shell becomes steeper, until an angle of about 90° with the plane of the anterior dorsal shield is attained. Around stage XII, the posterior edge bends and grows outwards into a brim. This differentiation of the shell sac is related to the differentiation of the mantle muscle (on the ventral side), as the latter is inserted on the lower face of this brim (Figure 15).

Up to stage XI, the shell sac shows no signs of any local excrescence or folding of either one of the epithelia. Around stage XII, however, both the primary and secondary epithelium present such phenomena.

In the posterior part of the shell sac, the secondary epithelium forms a lateral diverticulum on either side, in contact with the base of the fin rudiment. This process has been mentioned briefly by NAEF (1922). The lateral

pockets thus formed (Figure 10) correspond to those described in the sepiolid *Rossia macrosoma* (BOLETZKY & BOLETZKY, 1973), where the uncalcified shell is extremely reduced. Thus, independently of the presence or absence

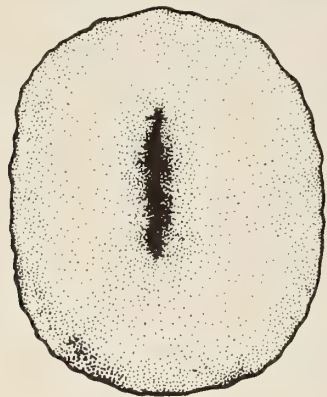


Figure 8

The early embryonic shell (protoconch) of *Sepia officinalis* often shows a ventral ridge or fold that is formed by the longitudinal fold of the primary shell epithelium shown in Figure 95

of a shell in the area of the fin base, the fin cartilage forms on the outer wall of these pockets.

The primary epithelium forms a groove that can become a very distinct deep and narrow slit, in which a ridge-like fold of the embryonic shell is anchored (Figure 8). It is not yet clear whether this acute form of epithelial depression does not occur in all embryos, or whether it is a short-lasting phenomenon that may occur sometime between stages XII and XIII; in fact, only part of the embryos preserved at these stages present a deep groove. Except for a very small infolding of the siphuncular epithelium, in which a tiny lobe of the first septum was anchored, this sort of groove has not been found after stage XIII.

From stage XII to stage XIV, the mantle and the shell sac grow considerably, and the primary shell epithelium becomes thinner. If large parts of it have appeared 2- to 3-layered at stage XII, most of it is clearly mono-layered epithelium by stage XIV. It is conceivable that this rapid stretching is partly prepared by the formation of a groove that would represent a "surface reservoir." The apparent irregularity of this process is not so surprising if one considers the range of variation in the other

Explanation of Figures 60 to 73

(Figures 60 to 73 are taken from *Spirula* shells)

Figure 60: View onto the apertural surface of the septum demonstrates lamellar crystal growth with somewhat dendritic components

× 8800

Figure 61: Septum broken nearly parallel to the growth surface shows the lamellar layers composed of needles arranged parallel to each other within each layer, but not so in neighboring layers

× 1500

Figure 62: View onto the peripheral portion of the apertural side of the septum shows continuously coarser crystals transitional between the lamellar structure and the prismatic structure

× 3900

Figure 63: Detail of Figure 86 showing the short brick-like crystals that are arranged vertical to the axis of the pillars which they compose

× 9500

Figure 64: The opened initial chamber of the shell showing the blind end of the siphuncular tube that continues as an organic sheet fixed to the opposite wall of the chamber

× 108

Figure 65: The end of the siphuncular tube with its organic cap that continues as an organic sheet

× 1000

Figure 66: The end of the siphuncular tube comprises the organic cap and the calcified portion with lamellar structure (detail in Figure 73). The tube is fixed to the outer prismatic shell wall in the constriction between the first and second chamber by a prismatic ridge (central right side). The inner tube of the siphuncle is filled with a secondary organic deposit

× 320

Figure 67: Section through the outer shell wall with the outer prismatic layer on the lower side of the picture and the coarse inner

prismatic layer at the upper side. The lamellar central layer forms the bulk of the shell

× 550

Figure 68: The entrance into the pillar zone of the second portion of the siphuncular tube extending into the blind initial section of the siphuncular tube already shows the typical apertural pillars, as at later stages. The length of this first pillar zone is much smaller than in later sections, however

× 350

Figure 69: A septum with its septal neck is broken to show the continuity of the siphuncular tube extending into it. At the entrance into the pillar zone, organic sheets are seen that had separated the liquid held in the pillar zone from that present in the chamber

× 130

Figure 70: The entrance to the pillar zone is formed by biconical solid pillars with 10 to 15 annulations; note free space between them. Their end on the inner siphuncular tube is fused to form a solid layer (see Figure 71).

× 175

Figure 71: The inner side of the inner siphuncular tube below the entrance to the pillar zone shows the solidly fused pillar ends against the (apically) following porous crystal cover of the pillar zone

× 1500

Figure 72: Detail of Figure 67 showing the central portion of the outer shell wall that is composed of small brick-like basal units in a lamellar structure

× 4500

Figure 73: Detail of Figure 66 demonstrates the lamellar structure of the end of the siphuncular tube (left). The latter is attached to the prismatic outer wall (right) by a coarsely prismatic ridge

× 660





morphogenetic processes going on in the embryo. All through these stages of later organogenesis, one will rarely find 2 embryos that are exactly identical in their morphological features.

The fast growth of the shell sac is reflected by the increments that are broadest in the anterior part of the shell; they measure between 0.03 and 0.08 mm each. In addition to these growth lines, there are several other morphological features that characterize the purely organic shell between stages XIII and XIV. In the posterior part (protoconch area), a longitudinal groove or a pair of grooves can be made out (Figure 9). The corresponding

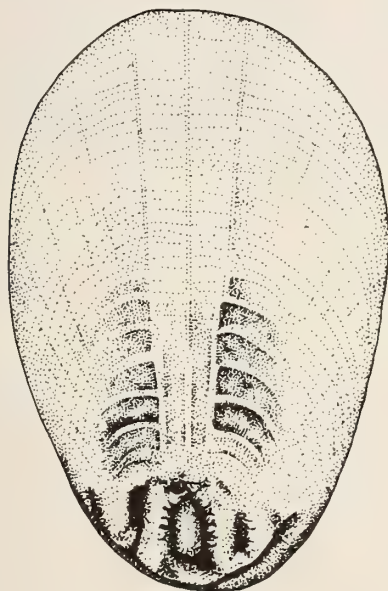


Figure 9

A later stage of shell formation in *Sepia officinalis*, before the onset of calcification. The protoconch area is marked by a depression that is surrounded by radial wrinkles. Along the growth lines, pairs of grooves appear, combined with radial ridges

form of the shell epithelium has apparently resulted from the folding and stretching processes mentioned above. The depressions in the shell are sometimes surrounded by radial wrinkles; occasionally there are also concentric wrinkles (Figure 9). On newly added portions of the organic shell, one finds radially arranged sculptural ridges. These become increasingly distinct with the growth of the organic dorsal shield. More laterally, one finds grooves that are

generally forming pairs arranged along the growth lines. Seven to 11 such pairs of crescent-shaped depressions have been found on different embryonic shells just before the onset of calcification (Figure 74).

In the organic shell of embryonic *Sepia pharaonis*, these morphological features were not found. There is only a central depression or a pair of depressions in the protoconch, and at later stages the shell shows only growth lines.

During the phase of mainly marginal shell growth described above, the marginal zone in the anterior and lateral parts of the primary epithelium is characterized by particularly high cells. This rim of columnar cells remains a typical feature of all the later stages of shell formation (Figures 11, 18).

Calcification of the embryonic shell begins between stages XIV and XV, when the shell has a length of about 2.3 mm. The first aragonitic layer is formed on the inner, ventral side of the shell, which it covers entirely except for a narrow marginal rim; the sculpture of the organic shell is thus fixed in its form. The radial ridges on the dorsal shell surface become distinct (Figure 45).

In its first phase, calcification is restricted to the ventral side of the dorsal shield, where a continuous layer of minute aragonite crystallites that form needle lamellae is deposited. This is the basement for the first pillars that are formed around stage XV.

In histological sections, the embryonic shell is usually distorted and often partly broken, and the closed shell sac balloons during fixation. It is often difficult therefore to relate shell structures to morphological and cytological features of the shell sac epithelium. However, the site of pillar formation is generally marked by a depression in the epithelium, so that it is easy to reconstruct the original position of the shell if it is well preserved. The question is whether these depressions reflect an actual cytological differentiation into "pillar forming cells," or whether they are insignificant or even artificial, the depressions being merely imprints of the pillars (preserved during the early part of fixation, before the shell sac expanded). Our observations suggest that these depressions are not significant for the mode of pillar formation. For these observations, it is crucial to have encountered optimal conditions of fixation, so that the shell structures are well preserved.

If the last-formed section of a chamber has, at least partly, been covered by an organic membrane when the animal was fixed, the "liquid" contents of the cavity next to the primary epithelium may be preserved in their original state. One then finds a stratification, which can only be made out by the refractive lines that mark the interfaces of the unstained layers (Figure 12). Thus there appears to be a stepwise secretion of the medium in which

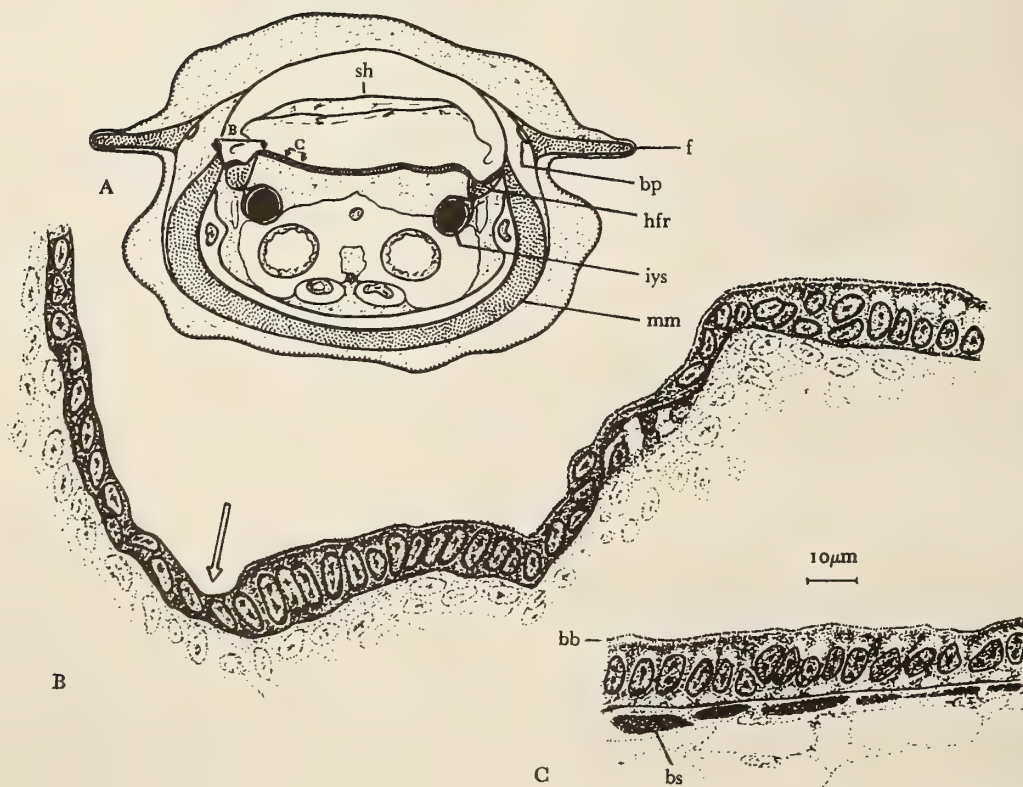
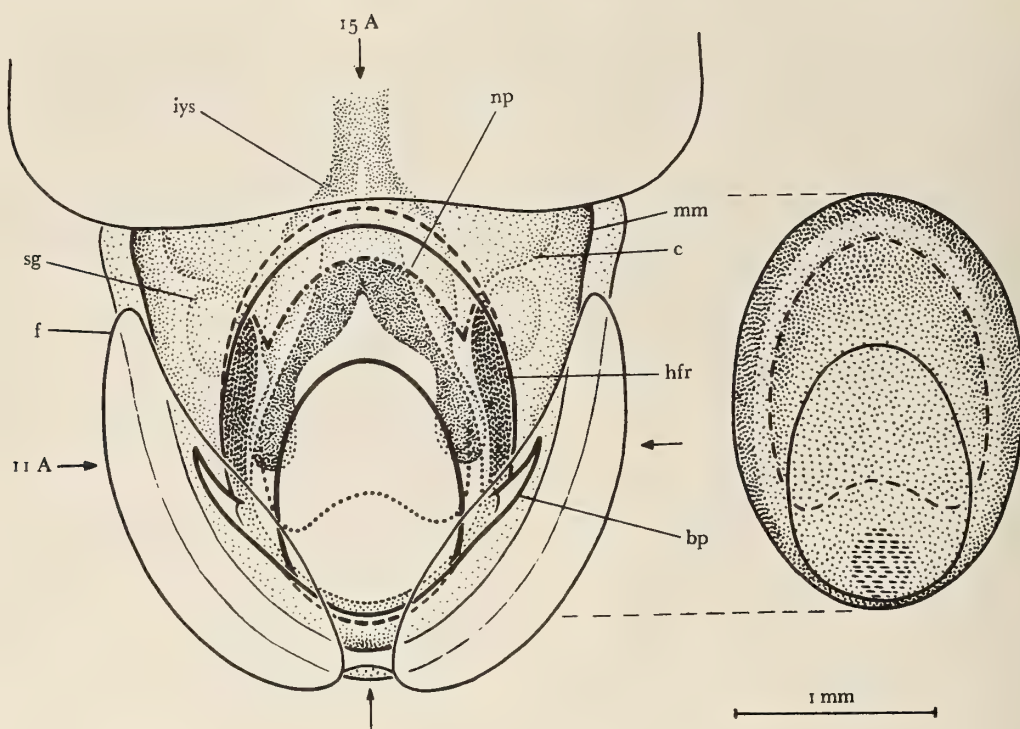


Figure 10

An embryo of *Sepia officinalis* at stage XVI of Naef. The pallio-visceral complex is reconstructed from cross-sections. Of the visceral mass, only the inner yolk sac (iys) is represented as the lowermost organ visible in this dorsal view of the body. The uppermost parts are the fins (f) with their basal pockets (bp) that are a differentiation of the secondary shell sac epithelium. In the shell sac, the embryonic shell is represented with its first complete chamber (broad oval line, at left), and the posterior part of the outline of the second chamber in formation (dotted line, at left). The broken line with dots marks the depth of the nuchal pouch (np). The insertion of the head and funnel retractors on the marginal part of the primary shell epithelium is marked by dark stippling (hfr). The mantle muscle (mm), the funnel pouch or collar (c) and the stellate ganglia (sg) are also indicated. The pairs of arrows indicate the plane of the section presented in Figure 11A and in Figure 15A. At right, the shell is represented with its first chamber and the outline of the second chamber in formation (broken line). The adhering primary epithelium is represented by the stippling, darker parts marking high columnar cells, lighter parts lower cells. The oval dashed field in the posterior part indicates the typical siphuncular epithelium.

(← on facing page)

the pillar lamellae crystallize, layer after layer. The fact that the unmineralized part of these layers is preserved suggests that they are gelatinous for some time after they have been secreted by the epithelium. These observations support the hypothesis put forward by BANDEL (1977a), according to which nacreous and lamellar layers form via a gelatinous phase.

On the solid, mineralized basement covering the ventral side of the embryonic shell, the first round pillars are set.

(← on facing page)

Figure 11

Cross section from the embryo shown in Figure 10 (camera lucida drawings). A: an entire section of the posterior part of the body (cf. arrows in Figure 10). The vertical expansion of the shell sac with the shell is an artifact. The arrow lines B and C mark the parts represented in the detail views (other abbreviations as in Figure 10). B: marginal part of the shell sac. The arrow indicates the limit between the secondary (left) and the primary shell epithelium (right). Note the similar height, but different aspect of cells in the marginal zone forming the organic rim and the middle zone (C and right part of B) where chambers are formed. C: the chamber forming epithelium shows a particularly distinct brush border (bb) with very long microvilli. Under this epithelium lie extensive blood spaces (bs).

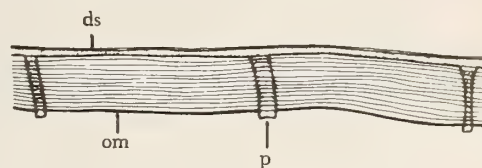


Figure 12

A schematic presentation interpreting the aspect of chamber contents as shown in Figures 96 and 97. When the animal was fixed, the shell epithelium had secreted what appears to be an organic membrane (om) and one or two gelatinous layers that have not been preserved except where crystallisation of pillar layers (p) had taken place. Between the dorsal shield (ds), in this particular situation (or an organic membrane or a septum, in general), and the organic membrane (om), the presumably gelatinous contents of the chamber are preserved and exhibit a periodical striation that is particularly distinct in the vicinity of the pillars (cf. Figures 96 and 97) where it appears to match the sequence of "nodular" thickenings.

Throughout their growth, only the uppermost portion shows mineral apposition, whereas further towards the base, they do not grow in thickness. These pillars are randomly distributed on the chamber ceiling, only the foremost ones forming walls that are radially arranged (Figure 75). Pillars are most densely set in the presumptive siphuncular area; they remain columnar in this posterior part of the chamber, whereas more anteriorly situated ones change in form during their growth. The latter measure about 10 μm in diameter; they have transversal bands, and their growth face has a central groove (Figure 77).

In the first chamber of *Sepia orbignyana* and *S. elegans*, the pillars are similar to those of *S. officinalis*. In *S. pharaonis*, however, the pillar base is often branched. The middle part of these pillars is again columnar (Figure 78). Between these growing pillars, the chamber roof is usually covered by a thin organic sheet; such sheets may also be extended vertically between pillars (Figure 79), so that the first chamber already has a labyrinth-like partition.

When the pillars have grown to a length of about 15 to 30 μm , an additional organic sheet is formed; it is extended horizontally between the pillars. When viewed from the ventral side of the shell, such a sheet may cover most of the chamber, except the marginal parts (Figure 76). In the first chamber, 4 to 7 organic sheets may be formed in the central part, in *Sepia officinalis* as well as in *S. pharaonis* (Figure 80).

Towards their apices (in the direction of growth, *i. e.*, towards the ventral end), the pillars change from their initial columnar form to a more wall-like structure. Near the chamber floor, these flattened pillars branch and form crenulations which may come close to those of neighbouring pillars. Thus the chamber floor shows a characteristic pattern of meandering lines (Figure 80).

The siphuncular zone of the first chamber is a small oval field (Figure 76). It differs from the anterior part of the chamber only by a denser distribution of pillars. The siphuncular area of every following chamber is a crescent-shaped band that shows the characteristic structure known of the cuttlebone (Figure 83).

The tendency of the pillars to form wall-like structures increases throughout the growth of the shell, but even in adult specimens, one always finds some columnar pillars within the actual chambers; in the siphuncular area, this remains the typical pillar form in *Sepia officinalis*, *S. orbignyana* and *S. elegans*. In *S. pharaonis*, wall-like and columnar pillars may alternate in one and the same meandering row of pillars.

The height of the embryonic chambers measures from 0.5 to 0.8 mm; this corresponds to the chamber height of juvenile individuals. The first chamber formed after hatching is often markedly lower, however.

The first calcification of the dorsal shell surface appears only after a few chambers are formed, *i. e.*, around stage XVIII. Aragonite crystallites of about 0.5 μm appear in a random pattern on the surface of the dorsal shield (Figure 37). Prominent sculptural elements, such as radial ridges, wrinkles and growth lines, are covered first. Thus they become very distinct for some time (Figure 45). Later on they will be covered by newly-added aragonitic layers.

The crystallites of this initial dorsal cover do not show any particular orientation. They grow along with the formation of interspersed organic fibers (Figure 37). Except for the margin of the dorsal shield, the entire dorsal surface is rapidly covered by a continuous layer of aragonite crystals; the spherulitic arrangement typical of this dorsal layer is soon established.

In *Sepia officinalis*, the posterior region of the embryonic dorsal shield is first covered by the same initial layer as the anterior part. The earliest traces of a spine appear only towards the end of embryonic life. The first crystallites that build the rudimentary spine are aragonite aggregations very similar to those forming the embryonic dorsal layer (Figure 39). The spine forms behind the protoconch grooves that can still be made out through the mineral cover.

Explanation of Figures 74 to 85

Figure 74: The embryonic shell of *Sepia officinalis* before calcification shows a central depression in the area of the protoconch. Following the initial shell cap radial sculpture elements and paired grooves situated in the growth lines have been formed when the shell was still free of mineral deposits. First mineral deposits (detail in Figure 45) fix these morphological features

× 28

Figure 75: Ventral side of embryonic shell of *Sepia officinalis* during formation of the first chamber shows the random pattern of the pillar insertion, with exception of the radially arranged foremost ones that form walls

× 42

Figure 76: The central portions of the embryonic shell of *Sepia officinalis*, towards the end of formation of the second chamber, is covered by a continuous organic sheet of the last intracamerallamella. The siphuncular zone of the first chamber shows up as a small oval field

× 30

Figure 77: Pillars in the central portion of the first chamber in *Sepia officinalis* show a growth face with a central groove. They project over an organic sheet suspended between them and are connected by vertical organic sheets

× 730

Figure 78: The pillars of the first chamber of *Sepia pharaonis* show a branching base turning into a columnar shape. The annulations of the pillar are clearly visible

× 1 200

Figure 79: Pillars of the first chamber of *Sepia pharaonis* connected by a vertical organic sheet

× 1 300

Figure 80: The round and the wall-like pillars of the first chamber of *Sepia officinalis* are crenelated near their ends in the septum. Organic sheets form 4 floors. The first septum has not yet been secreted

× 130

Figure 81: Round pillars at the first chamber of *Sepia officinalis* branch before they turn into the chamber floor

× 370

Figure 82: Fracture through a septum of the chamber zone of *Sepia gibba* showing the lamellar chamber floor and the prismatic chamber roof with a pillar rooted on it. Organic membranes do not cover the roof or floor surface, but are expanded through the chamber room

× 1 250

Figure 83: The embryonic shell of *Sepia pharaonis* during formation of the 6th chamber, after which the embryo would normally hatch. In the siphuncular zones of the chambers the organic covers are partly rolled up, exposing the posterior end of the chamber (details in Figures 34, 35, 36)

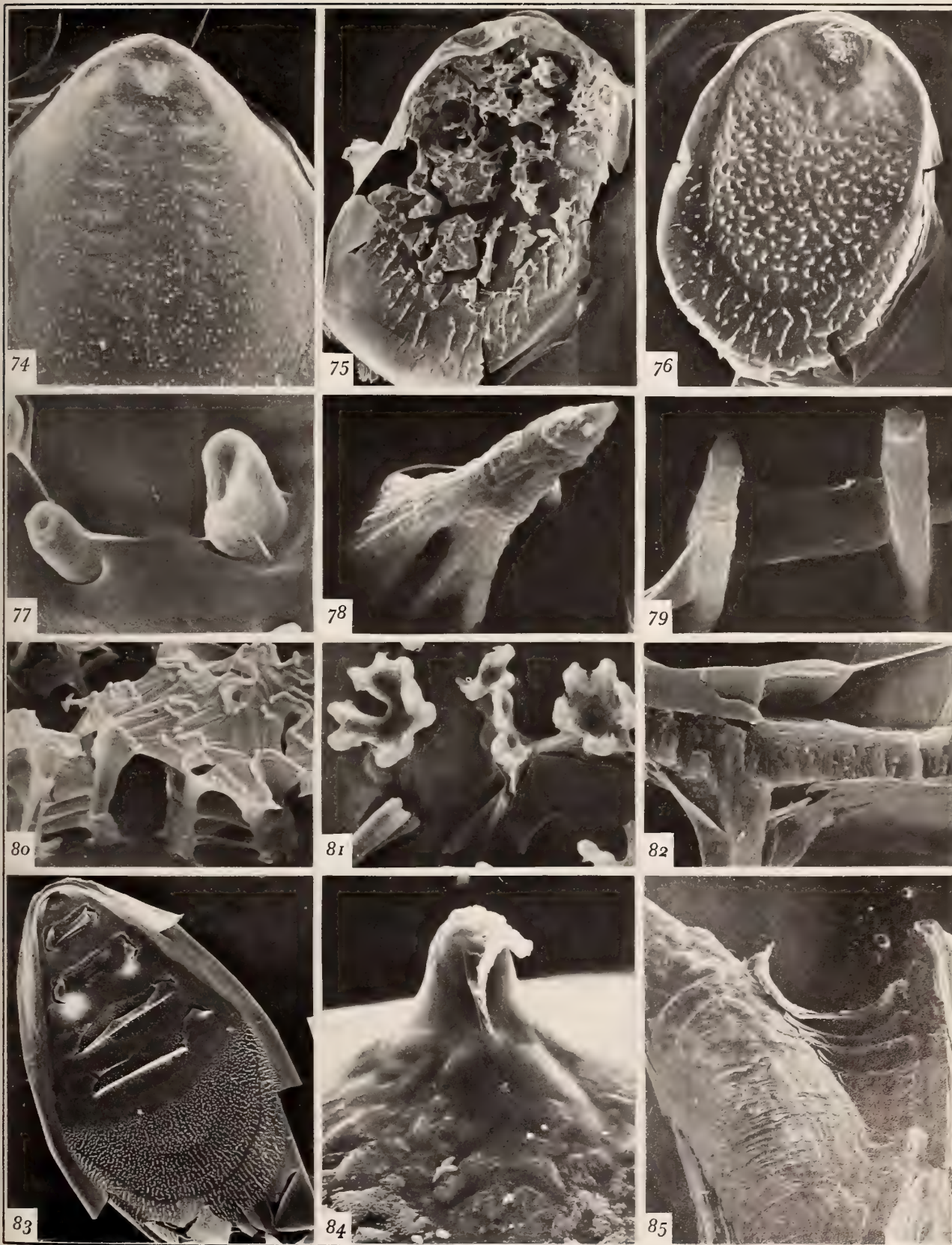
× 12.5

Figure 84: The spine of the hatching *Sepia pharaonis* is partly covered by organic material. Detail of base in Figure 57

× 620

Figure 85: The spine of *Sepia officinalis* is composed of lamellar structure which at the spine margins shows a rapid transition into purely organic sheets; these continue across the spine cover into the uncalcified portion of the central layer. For detail see Figure 41

× 19



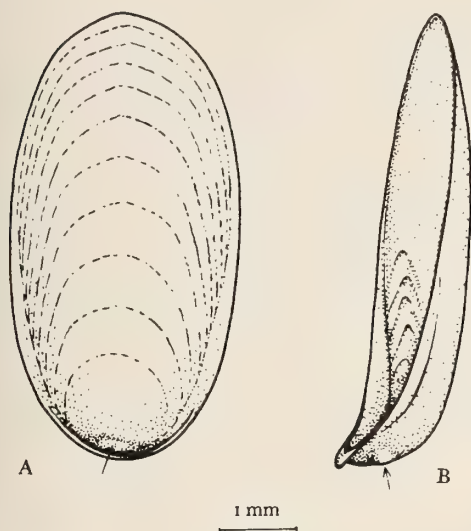


Figure 13

The cuttlebone of a newly hatched *Sepia orbignyana*. The rudiment of the spine (arrow) is barely visible on the rounded posterior part. A: dorsal view; B: ventro-lateral view

It is interesting that the spine is not yet formed in the newly hatched animals of *Sepia orbignyana*, a species with a very prominent spine in the adult stage. In the youngest animals, one only finds an inconspicuous thickening at the site where the spine will later form (Figure 13).

In *Sepia pharaonis*, the embryonic dorsal layer begins to develop in the form of a series of dispersed crystallization centers, where aragonite crystals aggregate into complete spherulites. These may fuse in the central part of the dorsal shield, whereas near the margins they remain isolated (Figures 14, 40). These spherulites consist of needle-like crystallites that radiate from the center of the nodules, which are 12–50 μm wide. They are embedded in the organic sheets of the outer and marginal shell layers of the embryonic dorsal shield.

In the region of the spine, the shell of embryonic *Sepia pharaonis* also differs from that of *S. officinalis*. Towards hatching, *S. pharaonis* has completed 6 shell chambers (Figure 83); this is less than in hatching *S. officinalis*, but the spine is already a large and solid structure (Figure 84), whereas in newly hatched *S. officinalis* it just begins to form. In the spine region of *S. pharaonis*, the crystal needles show the same orientation within an aggregate; i. e., there is neither a spherulitic nor a random orientation (Figure 57). These crystallite aggregations tend to



Figure 14

Longitudinal section through the cuttlebone of an embryo of *Sepia pharaonis* (with 5 completed chambers), showing the spine (s) with lamellar structure, the prismatic dorsal layer (dl) forming spherulitic aggregates near the posterior rim of the shell, and the central layer

(cl) that is purely organic in the region of the early embryonic shell and then becomes partly mineralized. In the siphuncular zone (sz) of the second chamber, the space between the pillars is partly filled with aragonitic crystals that show an inorganic type of crystal growth.

flatten out, with the needle axes following the plane of the organic sheets next to them (Figure 57). Thus their structure is intermediary between the patterns observed in the dorsal and central layers, respectively. The needle-like crystals of these early spine structures measure $0.2\ \mu\text{m}$ in width, like those of the central layer. The spine of newly hatched *S. pharaonis* is often covered by organic material (Figure 84); it strongly resembles the spine of the adult shell, which is similar to that of adult *S. orbignyana*.

During the later embryonic stages, the different parts of the primary shell sac epithelium reflect the increasing complexity of the shell structures they form. APPELLÖF

(1893) described and figured several typical forms of shell-secreting cells of the adult cuttlefish. DENTON & GILPIN-BROWN (1961) described the micro-anatomy of the siphuncular wall of the shell sac. Finally some ultra-structural aspects of the primary epithelium in the anterior chamber zone were described by KAWAGUTI & ODA (1963).

SPIESS (1972) tried to relate the histological differentiations he observed at stage XVI directly to the different types of cells described by APPELLÖF (1893). With the completion of the first chamber before stage XVI is attained, the embryonic cuttlebone has indeed acquired the



Figure 15

Medial longitudinal section of an embryo of *Sepia officinalis*, at stage XVI of Naef (cf. Figure 10, arrows). A: Semi-schematic presentation of the entire embryo in a medial section. The arrow line B indicates the area enlarged in B. The thick arrows a, b, and c mark parts corresponding to those represented in Figure 16, from

a later stage (abbreviations as in Figure 10). B: Histological aspect of the typical siphuncular epithelium with the early basal infoldings (left part) and of the epithelium of the posterior brim of the shell (sh), the upper right part belonging to the secondary epithelium

main elements of the future buoyancy apparatus. However, several parts of the adult cuttlebone, such as the spine, the dorsal layer and the fork, are still lacking. Furthermore, a comparison with later embryonic stages shows that the histological differentiation in general is still in its early phase at stage XVI. Thus, *e. g.*, the siphuncular tissue (type D of the 5 cell types listed by SPIESS, 1972) only begins to take on its typical structure with the basal infoldings described by DENTON & GILPIN-BROWN (1961) (Figures 15B, 16A). Also the chamber-forming epithelium (type C of Spiess) will attain its adult structure after stage XVI (Figures 16B, 18B).

We do not agree, therefore, with SPIESS (1972) who states, without presenting any figures of later stages, that "the following stages up to hatching do not present any crucial change in the tissue of the shell complex," and that

there is only "an insignificant reduction of the height of cells in the primary epithelium." The contrary is true, as one may see by comparing Figures 11, 15 and 16. What is crucial in these changes is that they lead to structures that are very similar to the histological aspect of the adult tissue. From the figures presented by APPELLÖF (1893) and by KAWAGUTI & ODA (1963) it is clear that the cells forming the calcareous material of the chamber zone are high, columnar cells. The assumption of SPIESS (*op. cit.*: 197) that high cells always form uncalcified structures, whereas calcified structures are always built by cubiform cells, is untenable.

The semi-diagrammatic representation of the primary epithelium at stage XVI (Figure 10) shows the peripheral zone of the high cells that form the organic rim of the dorsal shield (cf. Figure 11B). Next to this peripheral

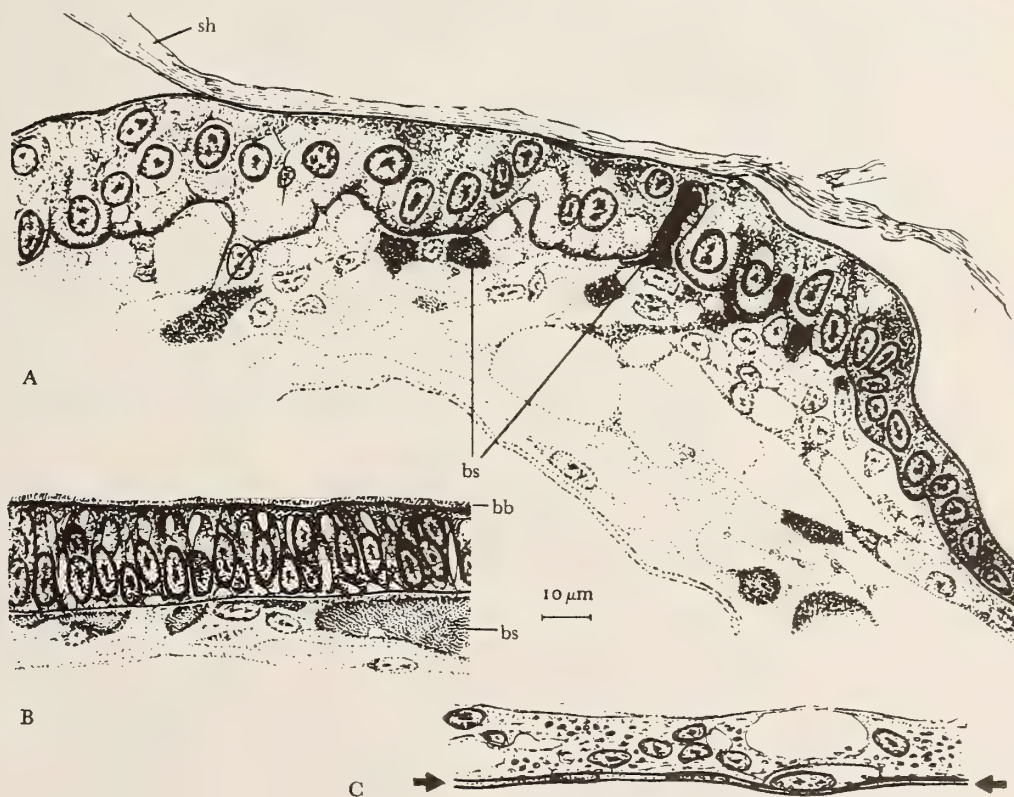


Figure 16

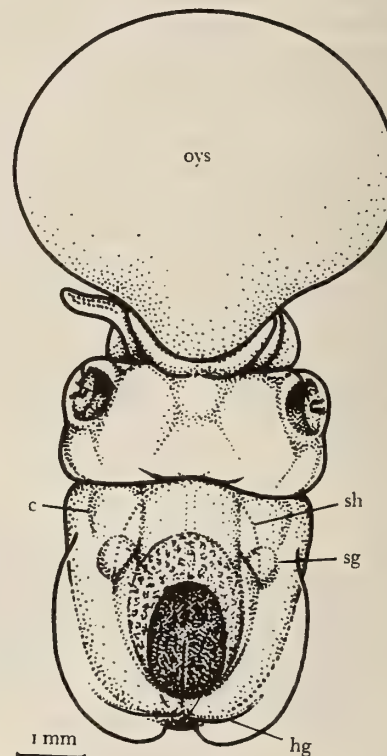
Sagittal sections from an embryo of *Sepia officinalis*, at stage XVII-XVIII of Naef (for their location cf. Figure 15). Note that these camera lucida drawings are at the same magnification as Figure 15B. A: the typical siphuncular epithelium, with the siphuncu-

lar wall of the shell (sh) adhering to it. B: the epithelium that forms the chambers, with high columnar cells and large vacuoles and a broad brush border (bb). The large blood spaces (bs) do not penetrate the epithelium, as they do in the basal infoldings shown in A. C: the extremely flat secondary epithelium (arrows!)

Figure 17

Embryo of *Sepia officinalis*, at stage XVII of Naef (dorsal view, drawn from living specimen). Note the large outer yolk sac (oys) which will be absorbed by the time of hatching when the animal will have doubled its size (cf. Figure 98). The shell (sh) has two complete chambers, and the third chamber is being formed. The anterior limit of the insertion of the head and funnel retractors can be made out by the position of the stellate ganglia (sg) (cf. Figure 10), which lie behind the collar (c). On the posterior mantle and fin surface lies the anchor-shaped hatching gland (hg)

(adjacent column →)



zone lies a band of very low cells that secrete the mineralized (ventral) marginal zone of the dorsal shield. The actual chamber-forming epithelium, however, is again composed of columnar cells, which are highest in the medio-lateral and anterior parts (Figure 10). The typical siphuncular tissue is rather limited and occupies an oval field close to the posterior end of the shell. This highly vascularized zone is surrounded by an area of apparently the same type of cells that do not form, however, the deeply folded epithelium that is so typical of the central part of the siphuncular zone (cf. Figures 16A and 18C).

The growth of the shell complex during the later em-

Explanation of Figures 86 to 94

Figure 86: Central pillar zone of *Spirula* broken open to show the septal neck (base of figure) with its lamellar structure. The pillars (detail Figure 63) are covered with the porous layer consisting of irregular crystals that line the inner space of the siphuncular tube. The lamellar structure of the pillar shows gradation into the irregular structure of the inner cover of the pillar zone $\times 1700$

Figure 87: The collapsed and then solidified end of the siphuncular tube of *Spirula* with its organic ribbon that extends to the opposite wall of the initial chamber $\times 350$

Figure 88: At the insertion to the outer wall (right) the septum of *Spirula* sits on a coarsely prismatic ridge. The septum is composed of well differentiated lamellar layers, which end abruptly at the prismatic ridge $\times 620$

Figure 89: The end of the siphuncular tube of *Nautilus pompilius* showing the first pillar zone on the nacreous inner wall of the initial shell cap. This pillar zone borders on the chalky layer at the margins of the siphuncular tube. The apical side of the first septum is seen in the lower part of the figure $\times 95$

Figure 90: The horny siphuncular tube of *Nautilus pompilius* ends in the spongy interfusion of the chalky layer and the organic sheets of the tube. This porous zone is in contact with the pillar zone

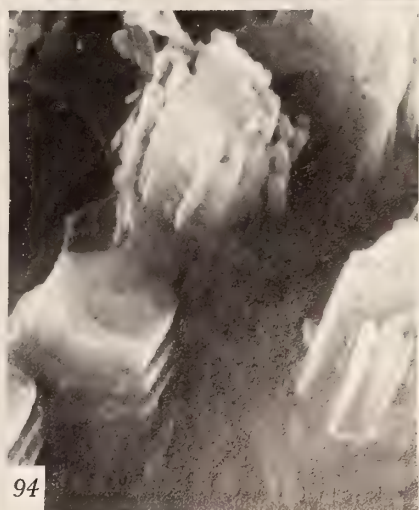
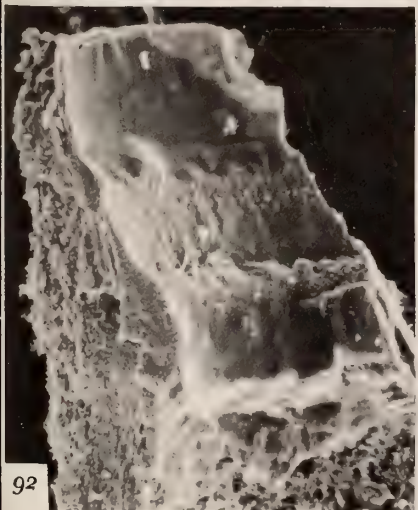
(Figure 91) within the septal neck. A chalky layer is not developed in this particular section of the siphuncular tube $\times 34$

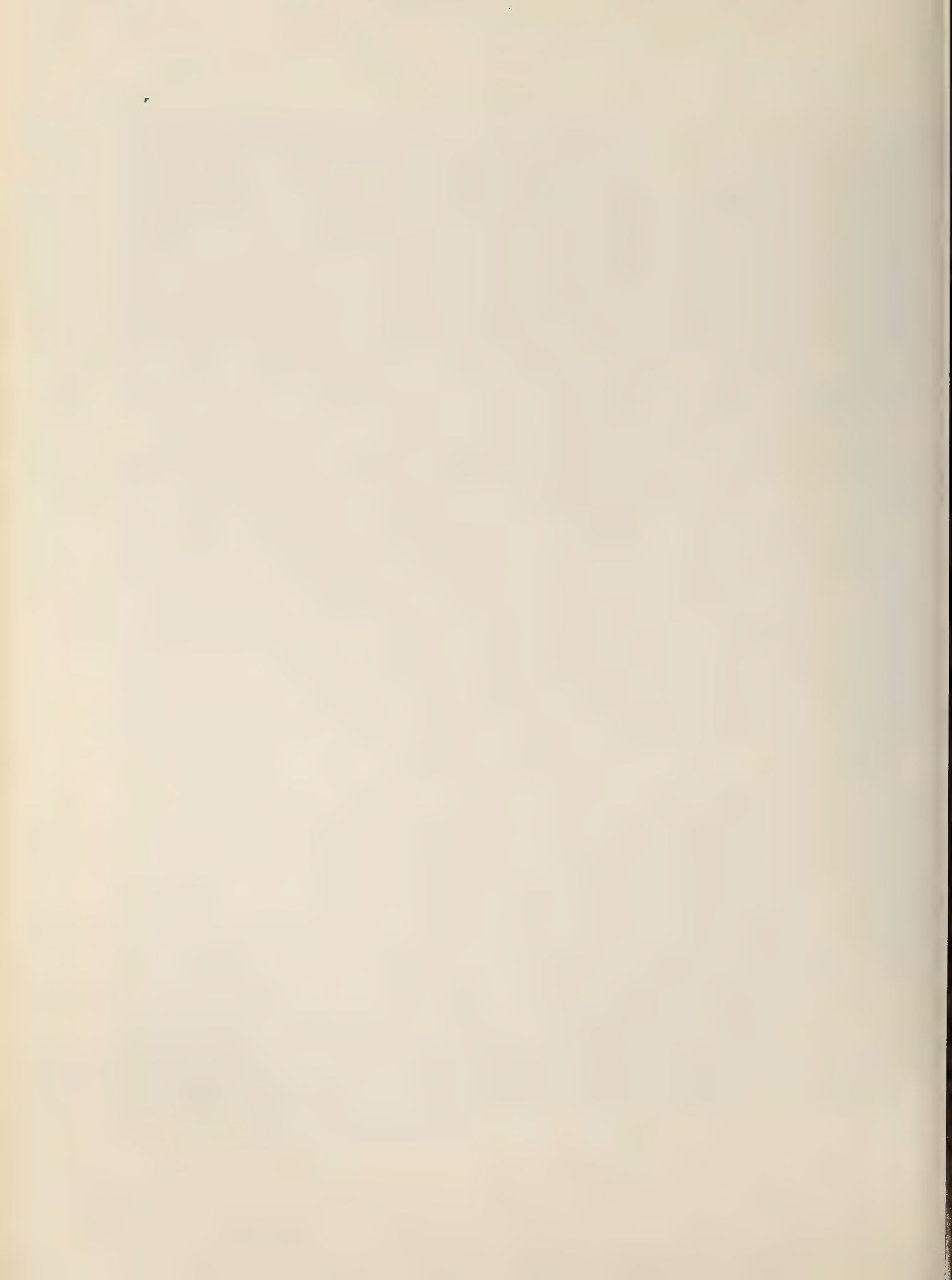
Figure 91: The inner side of the septal neck of *Nautilus pompilius* opened to demonstrate the inner non-porous ridge (upper portion of figure) covered by the organic sheet that continues into the horny tube (here torn off). The spongy apical end of the horny part of the siphuncular tube rests on the pillar layer seen in the central portion of the figure $\times 112$

Figure 92: A fracture showing the end of the septal neck of the siphuncular tube of *Nautilus pompilius*. The horny tube and the cover of the chalky layer are seen in the upper part of the figure. In the center is the non-porous ridge forming the attachment of the next section of the siphuncular tube. The tube is torn off near the base of the figure to show the end of the pillar zone $\times 82$

Figure 93: Crystals of the frontal pillar zone of the siphuncular tube of *Nautilus* show the transition from the lamellar nacreous layers into the prismatic pillars $\times 1500$

Figure 94: The inner pillar zone of the siphuncular tube of *Nautilus* shows the transition from stacks of nacre platelets to pillars of prismatic structure $\times 2950$





bryonic stages is most intensive in the anterior part of the mantle (cf. Figures 10 and 17), so that the insertion of the large head and funnel retractors continually approaches its definitive extent in the posterior part of the shell, on either side of the siphuncular zone (cf. TOMPSETT, 1939, for the anatomy of the muscular and other systems of the adult cuttlefish).

The secondary shell epithelium that forms the dorsal layer of the dorsal shield from stage XVIII onward remains very flat (Figure 16C). At its periphery, it becomes gradually thicker before it turns into the marginal part of the primary epithelium. In this outermost marginal area, the cuttlebone is firmly attached to the shell epithelium, which in turn is fixed via a delicate cartilaginous band to the dorso-lateral margin of the muscular mantle (Figures 10, 11B). The lateral pockets at the base of the fins (Figure 10) are gradually separated from the secondary epithelium.

When the animals hatch, their general aspect is very similar to that of the adult animal. However, the body proportions still differ markedly from those of the adult.

This is also true for the proportions of the shell; its width to length ratio is about 1:2 at hatching, against something like 3:8 at the adult age. Also the relative length of the last septum, which in young animals is shorter than the siphuncular zone, will increase during later development (MANGOLD, 1966). Only under artificial starving conditions will the last chamber always be shorter than the siphuncular zone; except for extreme starvation leading to constant positive buoyancy of the animal, these abnormal proportions of the chamber zone do not influence the buoyancy mechanism of the animal (BOLETZKY, 1974a).

We are still far from a detailed knowledge of the function at the cellular level of the different parts of the epithelium that surrounds the cuttlebone, builds its complex structures and forms the physical and physiological link between the other living tissues and the shell. In order to elucidate all the biological processes going on in the shell complex, a very detailed histochemical and ultrastructural study of the shell sac epithelium will have to be carried out on material that must be obtained under various well-defined experimental conditions.

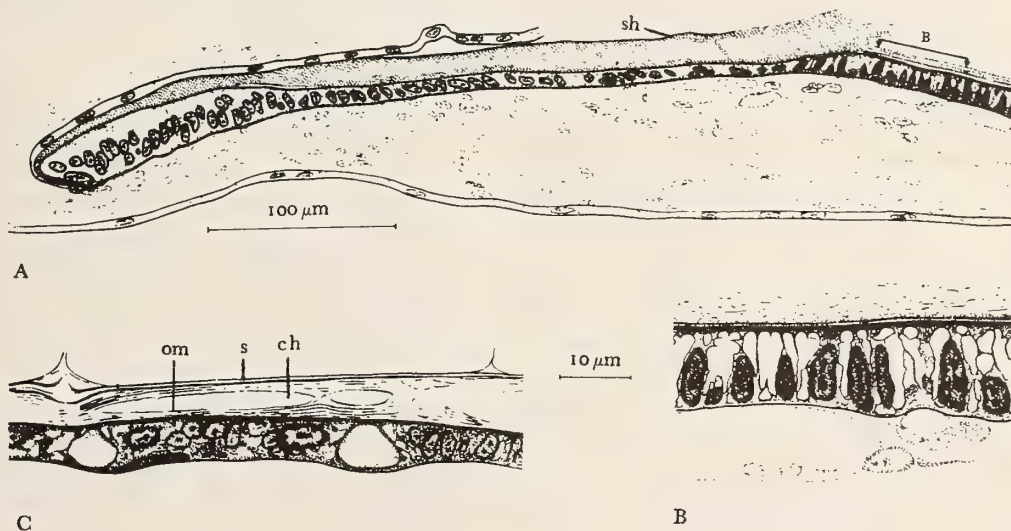


Figure 18

Sections from a juvenile *Sepia officinalis*, a few weeks after hatching. A: Cross section close to the anterior end of the cuttlebone. The left part of the shell (sh) is the organic rim (uniformly stippled). The middle part next to this shows artificial cavities due to the dissolution of calcareous shell material during fixation. At right is the peripheral part of the chamber zone, enlarged in B (cf. Figure 16B). C: Cross section from the lateral part of the siphuncular

zone in the same specimen. In contrast to the central part of the siphuncular zone, the epithelium is rather flat and shows no basal infoldings. It adheres to the organic membrane (om) forming the bottom of the chamber (ch) in the siphuncular zone. The small chamber height indicated by the next upper septum (s) shows that this section passes through the rearmost part of the chamber.

Development of the Shell Complex in *Spirula*

The embryonic development of *Spirula* is still unknown. It is also uncertain whether the smallest animals caught with plankton nets are newly hatched young. However, NAEF (1923, 1928) estimated from the size of mature ovarian eggs as indicated by CHUN (1910), that the newly hatched animals might have a total length of about 4 mm and that their shell would then have not more than 2 or 3 completed chambers.

In the Sepioidea so far studied, the dorsal mantle length of newly hatched animals corresponds roughly to the length of the mature ovarian egg from which they have developed. In *Spirula*, mature ovarian eggs measure 1.7 mm according to CHUN (1910). The smallest specimens we have been able to study, thanks to the kindness of Prof. Dr. E. J. Denton (cf. DENTON & GILPIN-BROWN, 1971), had a dorsal mantle length of about 2.7 mm, and their shell already had 3 complete (closed) chambers. The smallest specimens observed by CLARKE (1970) had a mantle length of only about 2 mm; probably they had not more than 2 closed chambers. If the newly hatched animals are markedly smaller, with a mantle-length of about 1.7 mm, it seems likely that they have only the first chamber closed, which measures 0.7 mm. Since in the known specimens the closed part of the shell never takes up more than half of the mantle length, one can practically exclude the possibility that the mantle complex that is markedly shorter than 2 mm holds a shell with 2 closed chambers. As only the posterior part of the digestive gland ("liver") occupies the open chamber ("living chamber"), the anterior part has to find its place in front of the shell, inside the mantle. In the smallest specimens we have seen, the posterior part of the head with the statocysts is also retracted into the mantle cavity, as in the adult.

It seems reasonable, therefore, to assume that *Spirula* hatches with the first chamber of the shell completed (and probably containing some gas to give the animal neutral buoyancy) — possibly with the second chamber completed, if the mantle-length of the newly hatched animal is not less than 2 mm (cf. Figure 19B).

JOUBIN (1910) and NAEF (1928) have clearly shown that the hypothesis of HUXLEY & PELSENEER (1895) postulating a partly external formation of the early shell in *Spirula* is untenable. Certainly the embryonic shell of *Spirula* is formed inside a closed shell sac that is more cup-shaped, however, than it is in other decapods. The early hypothetical stages figured in JOUBIN (*op. cit.*: figs. 15, 16) are not actually convincing, since the shell rudiment there appears as a narrow "pen" in the dorsal anterior part of the mantle, similar to the rudimentary shell of sepiolids. The following stage, however (stage III of

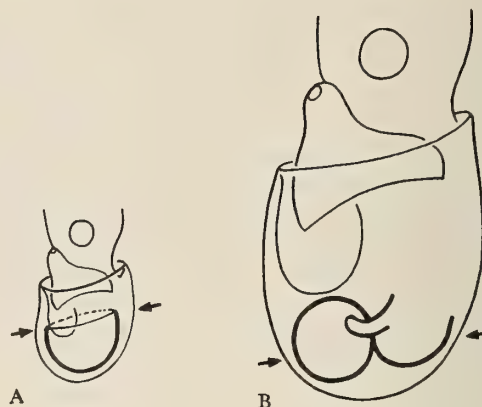


Figure 19

Hypothetical developmental stages of *Spirula*, after JOUBIN (1910, figs. 17 and 18). A: stage III of Joubin, with formation of the first chamber. At this stage, the embryo would have a large outer yolk sac. B: stage IV of Joubin, with formation of the second chamber. Arrows indicate the plane of insertion of the mantle muscle on the shell complex

JOUBIN, *op. cit.*: fig. 17) is likely to come close to reality. We have redrawn it in our Figure 19A. NAEF (*op. cit.*) suggested that in the early embryonic shell complex of *Spirula*, there should be some rudimentary formation representing the proostracum, which would disappear during later embryonic development. At any rate, the initial chamber does not show any trace of an early proostracum rudiment (which might simply be represented by the primary insertion of the dorsal part of the mantle rudiment on the margin of the shell sac).

What is important is that the insertion of the mantle muscle apparently "moves" from its primary location on the edge of the shell sac (where it probably lies at early organogenetic stages) to the outer surface of the shell sac, so that the first chamber can take up its position inside the muscular mantle. This displacement of the muscle insertion probably starts on the ventral side, but it also attains the dorsal side of the shell sac, the foremost part of which will then always lie under the muscle insertion. A comparison of Figures 19A and 19B may help to understand this process. Figure 19B (stage IV of JOUBIN, 1910) would represent a stage near hatching, according to our estimation of size and shell development.

With the further growth of the coiled shell, the displacement of the muscle insertion on the lateral and ventral parts of the shell complex continues, and early in

juvenile life the part of the shell sac that contains the first chambers becomes entirely detached from the mantle. The "movement" of the growing shell in relation to the mantle can best be compared to the movement of the innermost part of a spring in a clock-work that is being wound up.

The faster addition of shell material on the dorsal side of the shell as compared to the ventral side, which generates the spiral growth, seems to begin right after the formation of the protoconch; the posterior attachment of the "prosiphon" presumably lies in the protoconch area, and this attachment in fact lies on the ventral side rather than opposite the aperture (Figures 20, 64).

As we stated earlier, in the first chamber of the *Spirula* shell, the entire surface of the siphuncular tube is covered by a wrinkled organic sheet, from the aperture of the chamber to the line along which the "prosiphon" is attached to the wall (Figure 5). This organic sheet is the original embryonic siphuncular tube of the first chamber. Its formation and the subsequent modifications can be imagined to take the following course.

Before the siphuncle forms, the aperture of the first chamber is further constricted by a ring-shaped ridge that is secreted on the inner surface of the apertural constriction (Figure 20A). The formation of the second chamber has begun. As DENTON & GILPIN-BROWN (1971) have shown that only a small part of the new chamber wall is formed when the third chamber is closed, one can assume a similar situation for the closure of the first chamber.

Then the epithelium that has formed the prismatic wall of the first chamber separates from this wall, except for a line of attachment in the presumed protoconch area. It then secretes the organic sheet forming the first embryonic siphuncular tube while it is slowly retracted, the first chamber becoming filled with liquid (Figure 20B).

The next step is the formation of a calcareous tube that is wider near the apertural side than at its posterior end. The tissue of the siphuncle by then is well differentiated. The elastic organic tube, from which the tissue is now being removed, is apparently twisted near its (apertural) base before the calcareous tube is formed. The latter fixes the radial wrinkles resulting from this twisting movement, the significance of which is obscure (it reminds one of the hypothesis proposed by KERR, 1931, according to which the endogastric coiling of the *Spirula* shell had been brought about by the rotation of an originally exogastric coil, in some remote ancestor. This hypothesis appears rather imaginative).

The organic cap that closes the siphuncular tube is not sustained so that it may collapse (Figure 87). It either forms an edge on the end of the calcareous tube, or it re-

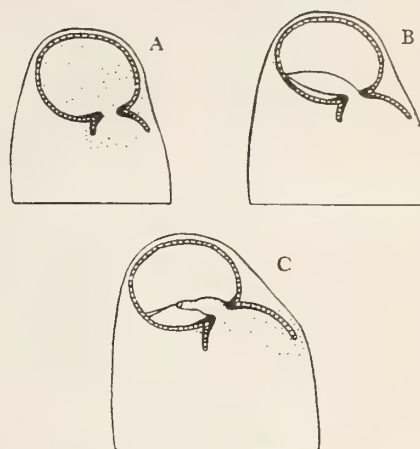


Figure 20

A schematic presentation of the processes by which the tissue withdraws from the first chamber of the embryonic *Spirula* shell.

A: the aperture of the first chamber is further constricted by a ring-shaped ridge. B: the epithelium that has formed the prismatic wall of the first chamber separates from the wall, except for the linear attachment in the (presumed) protoconch area. C: the calcareous tube forms after the siphuncular tissue has withdrawn from the elastic organic tube

tains its rounded cap-shape (Figures 20C, 64). This is fixed before liquid is extracted from the first chamber, which then becomes part of the functional buoyancy apparatus.

Development of the Shell Structures in *Sepia* and *Spirula*

The mineral composition of the shell of *Sepia* and *Spirula* is essentially the same. In both forms, aragonitic crystal-lites compose 3 types of layers:

1. the irregular structure made of aragonite crystals and crystal aggregations;
2. the regularly constructed prismatic layer;
3. the more complex lamellar layer.

Type 3 forms the major part of the shell wall in *Spirula*, the whole septum and the anterior part of the siphuncular

tube. The pillars of the posterior part of the siphuncular tube of *Spirula* also show the lamellar structure, like those supporting the chamber septum of *Sepia*. In the latter, the calcified parts of the central layer including the spine, of the fork layer, and the septa of the chamber zone have a lamellar structure.

Type 2 is found in the inner layer of *Sepia* and, as a more regular type consisting of coarse needle crystals, in the inner shell wall of *Spirula*. Still coarser crystals are found in the constriction that forms in the inner shell wall of *Spirula*, before insertion of a new septum takes place. Irregular, coarse crystals in spherulitic prismatic orientation (type 1 - 2) compose the outer secondary layer of the *Spirula* shell, the dorsal layer of the cuttlebone of *Sepia*, and the crystalline covers that appear late in the ontogenesis of *Sepia* in the posterior part of the siphuncular zone. The last-formed sheets of the inner layer of *Sepia* show a structure of spherulitic-sector and are composed of thin crystal needles. In fractures made parallel to the sector axis, they have a feather-like appearance.

Type 1 forms the cover of the siphuncular pillars of *Spirula*, and the crystalline filling of the posterior-most part of each chamber in the siphuncular zone of *Sepia*.

The simplest form of aragonitic shell structure is represented by the crystal aggregations and the single crystals that form a loosely interlocking porous layer. The crystals of the early dorsal layer in *Sepia officinalis* and of the siphuncular deposits in *Sepia* and *Spirula* have this structure. They are the product of an undisturbed crystal growth from liquids or mucus rich in calcium carbonate, where the shell secreting epithelium does not influence crystallisation. Such crystals are known from many aragonitic mollusc shells where crystals grow very rapidly; for example, during formation of a first layer of shell septa in the apertural whorls of gastropods (BANDEL, 1975), or closure of other cavities in gastropod and bivalve shells

(BANDEL & HEMLEBEN, 1975), and also within cavities closed off from the living tissue after the animal has withdrawn from them and formed a septum. Without any contact with the living tissue, remaining liquid or mucus rich in calcium-carbonate may then form crystals of the same shape and size as crystals that occur in mucus or body liquid still in contact with the secreting epithelium. The crystals and crystal aggregations of the porous layers formed in *Sepia* and *Spirula* can, therefore, be considered as largely uncontrolled formation of aragonite with the inorganic type of growth (BANDEL & HEMLEBEN, *op. cit.*; BANDEL, 1977a). They are not to be considered as biocrystals in the strict sense of the term (*i. e.*, structures of higher organisation where crystals are not "allowed" to form in their typical crystallographic shape, with well-developed crystal faces).

Such an indirect pathway of crystallisation without contact with the shell-secreting epithelium must be taken by the aggregates and crystals that lie between the pillars of the posterior pillar zone in *Sepia* and in *Spirula*. In the latter there are drum-shaped, short pillars; in *Sepia* they are thinner, more columnar. In both forms, these pillars show the lamellar type of construction, which is of much higher organisation than the inorganic type represented by the crystals and crystal aggregations that lie between the pillars. In this siphuncular zone, the completed pillars are covered by organic sheets; these apparently are permeable to liquid loaded with calcium carbonate that is secreted by the siphuncular epithelium.

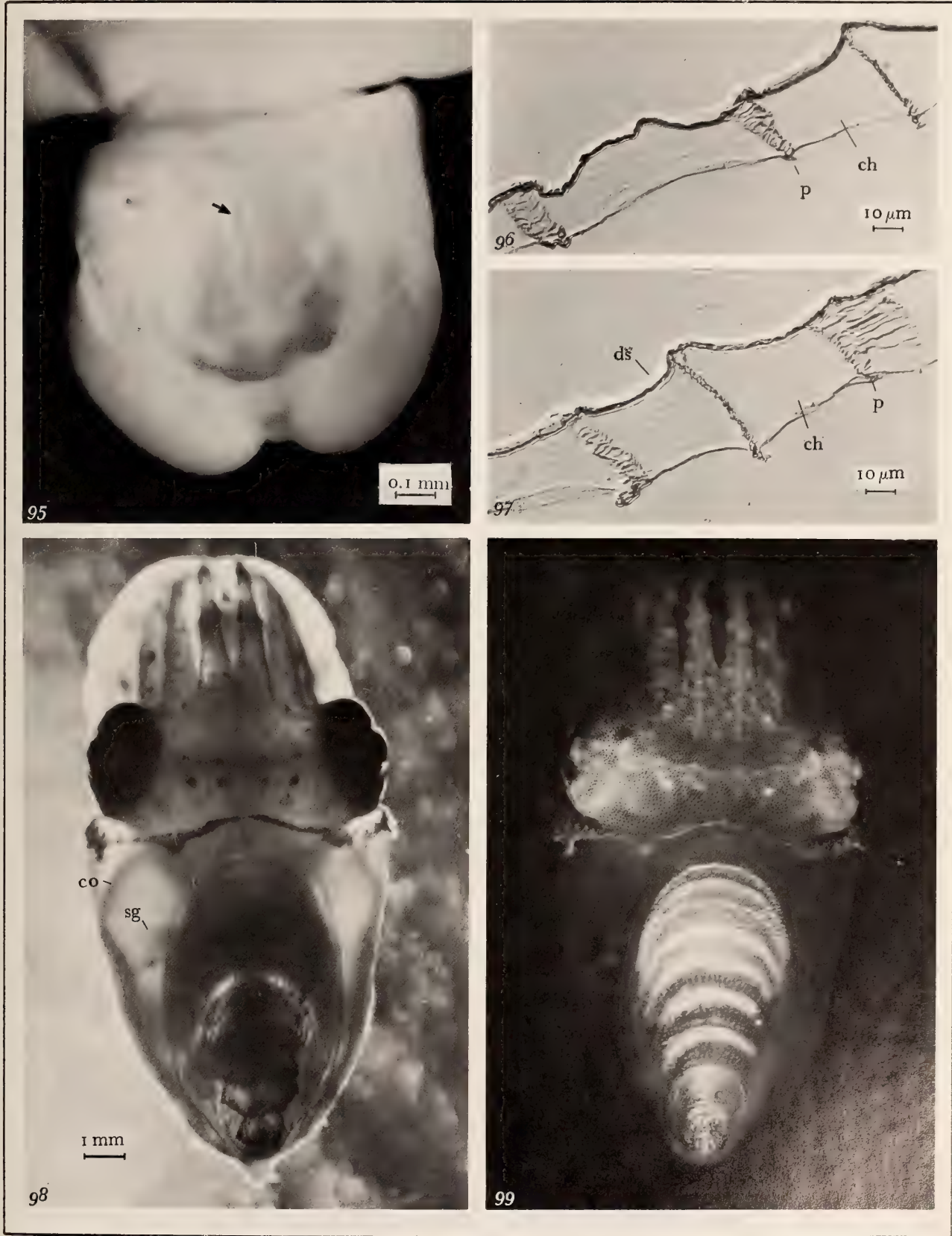
Crystals and crystal aggregations of inorganic fabric may also grade into the 2 types of higher structure present in the shells of *Sepia* and *Spirula*. In *Spirula*, the pillars of the siphuncular zone (posterior part of the tube) that are made of lamellae show a gradation into the irregular porous layer, via a transitional zone. The small, rod-like crystals of the pillar lamellae grow in thickness and become continuous across lamellae. Thus large crys-

Explanation of Figures 95 to 99

Figure 95: Dorsal view of the mantle of a *Sepia officinalis* embryo at stage XIII - XIV (fixed specimen). The dorsal part of the shell sac and the thin organic shell (cf. Figure 8) are removed to expose the primary epithelium. The arrow points to the longitudinal groove. Figures 96 and 97: Cross sections of the embryonic shell of *Sepia officinalis* at stage XVI of Naef (interference phase contrast photograph of histological section of material fixed in Bouin's solution). These sections are of the anterior part of the shell where the second chamber which is being formed lies under the dorsal shield (ds). The cavity of the chamber (ch) is filled with the future chamber liquid that appears still to be in a gelatinous state, exhibiting peri-

odical striation that matches the annulations of the pillars (p). (Note: the closed first chamber, not shown by these sections, does not present this striation between the pillars, probably because the chamber contents are already liquefied)

Figures 98 and 99: Newly hatched *Sepia officinalis*; anaesthetized live specimen. The skin of the mantle has been removed to show the shell complex, with the gas spaces of the cuttlebone showing up with a dark outline in transmitted light (Figure 98; co = collar, sg = stellate ganglion) and as bright reflecting surfaces in incident light (Figure 99)





tallites form in which lamellation is still visible at some distance until it disappears entirely. The crystals then show well-developed faces. The irregular layer following the highly regular pillar layer consists of crystals and crystal aggregates that are interwoven with organic fibers and sheets. As there is no alternation of crystalline material and organic sheets, the organic material must have polymerized in the interstices left between the crystals. It therefore seems likely that the organic shell material of these layers differs in composition and fabric from the organic sheets that are suspended between pillars, reflecting the different degree of complexity in their mode of formation.

The layer of irregular crystals and crystal aggregates resembles very much the first layers produced in the shell apex of certain marine gastropods, when a cavity is closed off by a septum (BANDEL, 1975: plt. 2, fig. 5). A continuous transition from lamellar layers (nacreous structure in this particular case) to crystal aggregates of inorganic fabric was found in the hollow spines of 2 archaeogastropod species (BANDEL, 1977a). In these cavities, pillar- or pyramid-shaped stacks of nacreous plates grade into crystal aggregations with a radiating structure. Similar transitions exist in the *Nautilus* shell (MUTVEI, 1972; cf. our Figures 93, 94).

The first irregular crystal cover, by which the formation of the dorsal layer in *Sepia officinalis* begins, also resembles the cover of crystal deposits in the shell repair of gastropods (BANDEL & HEMLEBEN, 1975). As in some gastropod septa, this layer grows into a prismatic or spherulitic prismatic structure with needle-like crystals of variable thickness that are oriented vertically to the growth face (cf. BANDEL, 1975: plt. 5, fig. 5; BANDEL & HEMLEBEN, *op. cit.*: figs. 2, 4, 11).

The dorsal layer of the *Sepia* and *Spirula* shell is made of crystal needles of different sizes; they either form a coarse prismatic layer, or spherulitic-prismatic ridges and bumps. The latter often show a radial arrangement of the needle crystals around the central base, in a spherulitic manner. The dorsal layer grows by mere enlargement of the needle crystals that show well-developed crystal faces. This kind of growth does not require much interaction with the shell-secreting epithelium. The latter creates a chemical micro-environment that favours the formation of aragonite and the final production of an organic cover to end the crystal growth.

The inner prismatic layer of the *Spirula* shell and the inner layer of the cuttlebone of *Sepia* show a spherulitic prismatic structure with a more regular arrangement of crystals than in the dorsal layer. But the influence of the epithelium on the mineral structure is still limited; crystals are large and show well-developed crystal faces. In

the lower part of the inner layer of *Sepia*, the width of crystals is smaller, and the spherulitic sectors they compose are more apparent than in the upper part where crystallites are broader. The needle crystals that grow on the inner surface in round bump-like structures are inclined towards a common central axis, thus forming columnar units. The single needles are crystals with well-developed heads at the growth face.

In contrast to the structures so far discussed, with crystals that may attain considerable size and that show crystal faces, the lamellar layer is composed of small elements (0.1 to 0.3 μm) that rarely show crystal faces. These elements are surrounded by and interlocked with organic shell material to a much greater extent than crystals are in other structures. These smallest units may be arranged in many different ways, but they always form a lamellar structure with lamellae strictly parallel to the growth surface. The thickness of lamellae varies from 0.1 to 15 μm . Lamellae are continuous over large stretches; we have rarely found a free end or a splitting. However, mineralized lamellae may turn abruptly into lamellar organic sheets. At the interface with one of the 2 other types of structure observed in *Spirula* and *Sepia*, lamellation sometimes continues a little into the other layer.

MUTVEI (1970, 1972a, 1972b) described the nacreous layer of *Nautilus* and *Mytilus* as being composed of small crystalline units that are very similar to those we find in the lamellar layer. The typical nacreous crystals are tabular and have a hexagonal outline; they are known from many species of gastropods, lamellibranchs and cephalopods (Recent *Nautilus*, fossil Nautiloids and Ammonoids). BANDEL (1977a) has shown that the smallest components of mature nacre are round or irregular rod-like elements, particularly visible on the sides of growing platelets. These smallest elements (0.2 μm) build platelets that have the optical properties of monocrystals. The nacre platelets described by MUTVEI (1972a) from the septum and the siphuncular tube of *Nautilus* have a highly variable intracrystalline structure. Variation is particularly great in the posterior end of the calcified septal neck, with platelets made of needles 0.1 - 0.2 μm in thickness, of dendritic crystallites or rods (MUTVEI, 1972a: pls. 15, 16). As in the lamellar layer, these crystallites are composed of smaller granules with a maximum diameter of 0.2 - 0.3 μm . But in contrast to the lamellar layer, these crystal laths build platelets with distinct margins. It is conceivable that the lamellar layer is a structure derived from nacre platelets of the type described by Mutvei from the posterior siphuncular tube of *Nautilus*.

Similar to what has been shown by MUTVEI (1970, 1972a, 1972b) and BANDEL (1977a) for nacre platelets, the lamellae of the lamellar layer may be composed of

needle elements lying parallel to each other, of dendritic crystallites with bifurcating branches, of rods parallel and perpendicular to the plane of lamellation, and of very small, irregular units. All components show the same basal unit with a size between 0.1 and 0.3 μm (as in different aragonitic layers of certain mollusc shells with crossed lamellae or with a helical structure; cf. BANDEL, 1977b).

In the hollow spines of the archaeogastropods *Guildfordia* and *Angaria*, BANDEL (1977a) found columnar nacreous structures that extend parallel into the central space of the spine. At their base, these pillars show mature nacre, followed by an increasingly coarse composition in subsequent platelets. In their uppermost part, the pillars are composed of coarse aragonite crystals. Lamellation continues through neighbouring pillars, and the lamellae are strictly parallel to each other. During their growth, the pillars are surrounded by liquids that are rich in calcium carbonate, and each nacre lamella continues to enlarge only according to its own structure, independently of the neighbouring lamellae. The closure of narrow spaces in the vicinity of these columnar structures during further growth is no evidence of the presence of membranes that should surround each lamella, thus restricting its type of growth to one specific structure, as postulated by the "compartment theory" (see ERBEN, 1974, and BANDEL, 1977a for a discussion of the two main hypotheses on the mode of shell formation in the molluscs). In an attempt to explain the difference in the respective type of crystal growth in the nacre of these pillars, from mature nacre to large crystals of inorganic fabric, BANDEL (*op. cit.*) suggested that lamellae of gelatinous matter, successively secreted by the epithelium, may form the medium in which the nacre platelets form. The chemical composition and the consistency of these gelatinous layers were thought to determine the composition and structure of the forming platelet.

Since the gelatinous lamellae may liquefy or be precipitated on the mineral shell components, they are generally not preserved by current fixation methods. However, our observations on the lamellar filling of newly formed chamber sections in the *Sepia* shell confirm the hypothesis of BANDEL (1977a) on the mode of formation of the lamellar structure in nacreous layers.

It must be emphasised, however, that the "chitinous" material which APPELLÖF (1893) observed in the last-formed chamber of cuttlebones is most likely the product of precipitation of the chamber liquid, rather than gelatinous layers not yet liquefied. These probably are liquefied in the upper layers of a chamber, separated to a large extent from the lower parts in formation by the horizontal organic sheets; so that only lower parts contain consistent gelatinous layers when the chamber floor is formed.

In the last-formed chamber of alcohol-preserved cuttlebones, we have indeed observed contents that recall Appellöf's description.

Homology of the Shell Constituents in *Sepia* and *Spirula*

APPELLÖF (1893) apparently realized that the entire chamber zone of the cuttlebone should be considered as homologous to the siphuncular tube of *Spirula* and *Nautilus*, as the chambers of both have pillars at, or close to, the inner side of the septal neck (we shall return to his observations on *Nautilus* further below). In *Sepia*, the chamber zone, together with the fork, would represent a greatly modified siphuncular tube with an extremely enlarged dorsal part (= chamber zone) and an almost completely reduced ventral part (= fork).

We have shown above that neither the number of fork layers nor the total number of lamellae that make up these layers correspond to the number of chambers. According to Appellöf's idea of the development of the *Sepia* shell, earlier forms like *Belosepia* of the Eocene would have been followed by forms with flatter and broader shells, until the ventral part became completely "compressed" in the posterior portion of the cuttlebone in *Sepia*.

NAEF (1922) also considered *Belosepia* as a transitional form in the evolution of the *Sepia* shell. He suggested that the outer wall of the phragmocone ("Conothek") took its part in the formation of the fork. In Naeff's reconstruction, the septal necks become flatter and the siphuncular tube widens until it is a shallow pit. The proostracum, still present in his reconstruction of *Belosepia*, disappears. According to Naeff, *Belosepia* is derived from ancestors like *Spirulirostra* and *Belemnosella*, which had a proostracum and phragmocones that were longer than in *Belosepia*.

We have been able, thanks to the kindness of Dr. L. Jansen (Leiden), to examine a well preserved Miocene representative of *Spirulirostra*. This fossil form closely resembles *Spirula*, except for the large rostrum. We have not seen any particular similarity to *Sepia*. Although the gross morphology of the siphuncular tube of *Spirula* is very different from the siphuncular zone of *Sepia*, it has been shown by DENTON & GILPIN-BROWN (1971, 1973) that in both forms the siphuncular complexes are alike. The shell wall and the septa are always impermeable to sea water and other aqueous solutions; the only permeable zones lie in the siphuncular tube of the *Spirula* shell and in the siphuncular zone of the cuttlebone. In *Spirula*, the permeable zone is restricted to the posterior part of the siphuncular tube, and in the cuttlebone it is restricted to the rearmost part of what we call chamber in the *Sepia*

shell. Thus the only connection between the liquid inside a chamber and the living tissue of the siphuncle is through the permeable organic membranes of these specialized zones of the siphuncular wall.

From a newly closed chamber the liquid is actively extracted while gases slowly diffuse into the chamber; this exchange is prepared by the removal of salt from the chamber liquid (DENTON & GILPIN-BROWN, 1966). When gas appears in a new chamber of *Spirula*, the salt concentration of the remaining chamber liquid is only $\frac{1}{2}$ of that in the blood and sea water (DENTON & GILPIN-BROWN, 1971a). This osmotic difference that is actively maintained by the siphuncular tissue counteracts the hydrostatic pressure; the volume of the gas spaces can thus remain nearly constant despite an increasing outer pressure when the animal descends into deeper water, the salt concentration of the chamber liquid being lowered with increasing hydrostatic pressure.

With the appearance of a gas bubble in a newly closed chamber, the main volume of chamber liquid is "de-coupled" from the liquid that is in contact with the siphuncular wall, so that short-lasting changes in hydrostatic pressure do not imply an adjustment of the salt concentration in the entire chamber liquid (DENTON *et al.*, 1961).

Spirula normally swims head down, and in this position the main volume of chamber liquid is de-coupled from the permeable region as shown by DENTON *et al.* (1971). These authors cite a personal communication of Clarke, who had observed that *Spirula* can reverse this position for some time, and conclude: "Thus in *Spirula* the main body of liquid within a recently formed chamber may sometimes be brought directly against the permeable region of the siphuncular tube. It remains true, however, that when *Spirula* is in its normal swimming position, this liquid will be almost completely de-coupled from the permeable region."

This problem of course does not arise with the cuttlebone of *Sepia* where the main body of liquid is distributed in the form of a fluid film covering the greatly enlarged inner surface of the chamber into which gas has diffused. And even in the newly formed chamber, "the exchange of salts between the liquid just inside the siphuncular surface and that deeper within the cuttlebone will be limited by diffusion" (DENTON *et al.*, 1961).

Neutral buoyancy is thus achieved in the pelagic *Spirula* and in the nekto-benthic *Sepia* by a regulatory mechanism the structural elements of which are very similar despite the different shell form. Although we have no direct evidence of a common ancestor of *Sepia* and *Spirula*, there can be little doubt of the homology of these structural elements that compose the permeable siphun-

cular wall and the "de-coupling" zone. In the *Sepia* shell, this zone with its pillars and organic sheets has completely "replaced" the actual chamber of the form that is represented by the *Spirula* shell.

SURVEY OF THE SIPHUNCULAR SYSTEM OF ECTOCOCHLEATE CEPHALOPODS AND OF THE BELEMNITES

In a series of studies, DENTON & GILPIN-BROWN and DENTON *et al.* (see DENTON, 1974 for complete list of references) have analysed the structure and functioning of the buoyancy apparatus of *Nautilus*, *Spirula* and *Sepia*, and they suggest that the mechanism by which liquid is pumped out of a newly formed chamber and gas diffuses into it must have been the same in all cephalopods with chambered shells, including the fossil nautiloids, ammonoids and belemnites.

Nautiloidea

In *Nautilus*, the chalky and probably also the horny parts of the siphuncular tube are porous. The respective volume of chamber liquid diminishes from the last chamber to the older ones, most of the chambers containing very little liquid (DENTON & GILPIN-BROWN, 1966).

The complete extraction of liquid from a chamber in *Nautilus* depends on the physical properties of the pellicle that lines the chamber and the siphuncular tube. This pellicle makes the walls wettable, and the chalky siphuncular tube acts as a wick that draws liquid uphill towards the siphuncular epithelium (DENTON & GILPIN-BROWN, 1966). The chalky siphuncular tube (spherulitic-prismatic layer of MUTVEI, 1972a), in addition to acting as a wick also serves as a small reservoir of liquid close to the siphuncular epithelium. An additional space for liquid lies between the pillar-like structures, which are set on the nacreous central surface of the concave septal face and are covered by an organic pellicle. This pillar zone extends a little into the septal neck and there comes into contact with the porous chalky layer.

The structure of the siphuncular tube of *Nautilus* has been described in some detail by APPELLÖF (1893). He found that the nacreous septal neck is continuous with the horny tube. The latter is covered on the chamber side by a porous calcareous layer, the "chalky layer" of DENTON & GILPIN-BROWN (1966). Where this compound tube enters the aperture of the next older septum, it makes contact with a crystal structure in the form of pillars that are clearly separated by interstices. Appellöf also noted that only on the inner side of the apical-most portion of the

septal neck a solid (non-porous) calcareous inner layer is formed, in which this section of the siphuncular tube ends.

MUTVEI (1972a) studied the siphuncular tube of *Nautilus* again in great detail. He showed that the single organic sheets that compose the horny tube are calcified close to their apical end, *i. e.*, inside the septal neck of the next older septum. Thus they are solidly fused with the inner side of this septal neck.

Our observation on the siphuncular tube of *Nautilus pompilius* Linnaeus, 1758 indicate that the horny tube splits into thin organic sheets before it reaches the non-porous calcareous ridge mentioned above. These observations differ from those of MUTVEI (1972a: fig. 2), who figures the horny tube without a change in its structure up to the solid inner ridge. Only in contact with this ridge the horny tube is shown to split into single sheets that are incorporated in the ridge. A reconstruction similar to that of Mutvei has been presented by BLIND (1976: figs. 5, 7).

Our Figure 21 shows the attachment of the siphuncular tube within the septal neck of the previously formed septum, with the horny siphuncular tube splitting into many sheet-like, discontinuous and irregular organic membranes before it ends in the solid inner ridge. In this part, the organic tube is interspersed with the irregular prismatic crystals that are present all through the chalky layer of the siphuncular tube; it has a spongy structure therefore (Figure 90). This structure is very likely more permeable to liquids than the actual horny tube, which is rather solid (Figure 22). In the pillar zone inside the septal neck, the pillars are widely spaced (Figure 94). This zone is in contact with the spongy end of the siphuncular tube belonging to the following chamber. So we find an arrangement of pillars and an irregular roof made of crystal aggregates and organic sheets very similar to what we have seen in *Spirula*. The porous area is much shorter than in *Spirula*, however.

Behind this spongy part, the organic sheets unite again, partly covering and partly penetrating the solid ridge

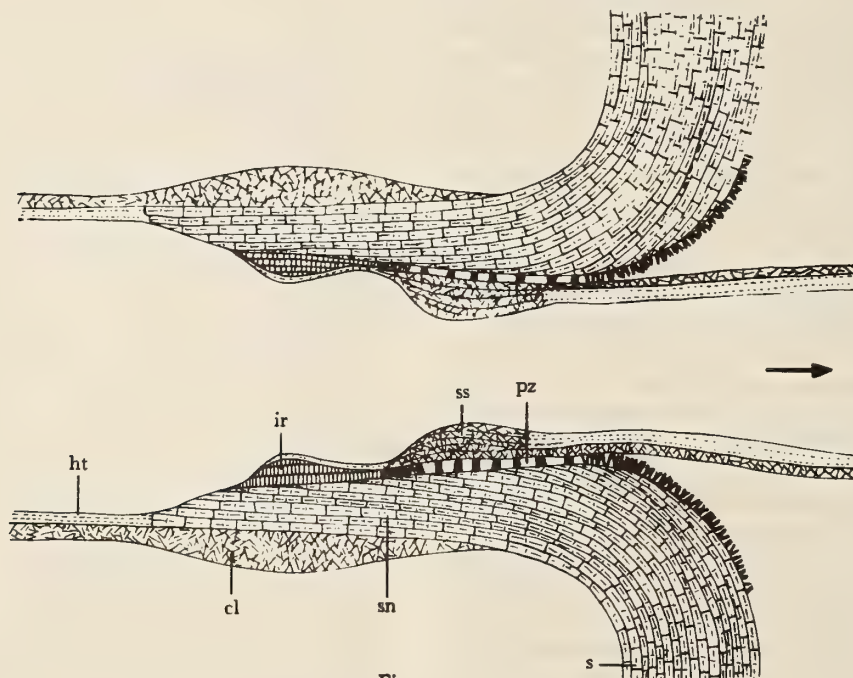


Figure 21

Longitudinal section of the siphuncular tube of *Nautilus pompilius*. The arrow points toward the aperture. The nacreous layers of the septum (s) continue into the septal neck (sn), the organic parts of which are continuous with the horny tube (ht). The septal neck and the horny tube are covered by the chalky layer (cl) which is a porous structure made of needle aggregates and organic sheets. The

apical end of each section of the siphuncular tube is firmly attached to the inner side of the septal neck by a solid inner ridge (ir). In front of this lies a porous spongy structure (ss) made of many discontinuous organic membranes interspersed with elements of the chalky layer. This spongy structure brings the liquid contained in the pillar zone (pz) into contact with the siphuncular tissue

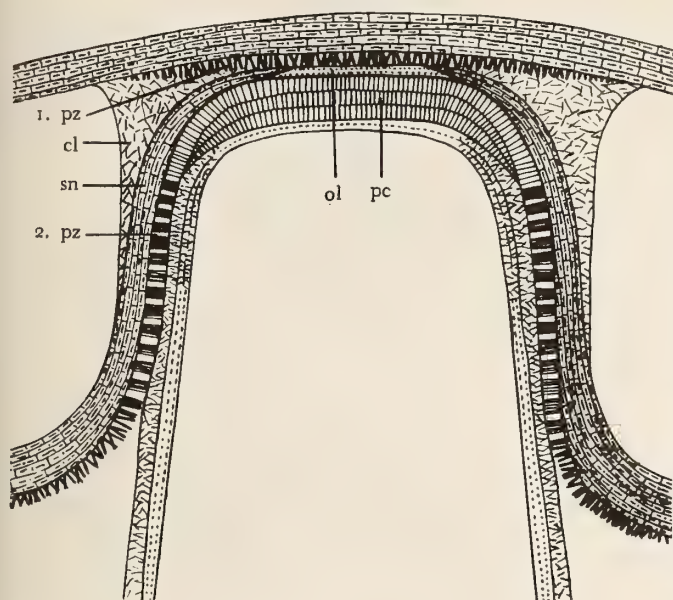


Figure 22

Section through the beginning of the siphuncular tube of *Nautilus pompilius*. The siphuncle makes contact with the inner side of the shell at the site of the earliest embryonic shell (protoconch). Between the nacre of the shell wall and the blind end of the siphuncular tube lies a porous, prismatic first pillar zone (1st pz). In the central part, this zone is covered by an organic layer (ol), and in the peripheral parts by a chalky layer (cl) made of organic sheets and prismatic crystallites. The nacreous septal neck (sn) extends to the porous first pillar zone, through which the liquid of the first chamber is pumped out before more shell material is deposited with the formation of the following section of the siphuncular tube. The latter forms a solid prismatic cap (pc) closing the porous end of the siphuncular tube. The second pillar zone (2nd pz) corresponds to what is formed in later parts of the tube

(Figures 21; 91, 92). DENTON & GILPIN-BROWN (1966) showed that the siphuncular tube of living *Nautilus* is porous. Their experiments were carried out in such a way that more or less porous zones would not be differentiated along the tube. The structure of the siphuncular tube now clearly shows that the most porous zone lies at the apical end of each tube section. There the liquid that is in close contact with the siphuncular tissue is retained in the interstices between the pillars; thus it is de-coupled from the main body of chamber liquid.

The beginning of the siphuncular tube is shown in Figures 22 and 89. Different reconstructions of this feature

have been presented in the literature. MUTVEI (1964, text fig. 26; plt. 14) has found an outer spherulitic-prismatic layer corresponding to the outer chalky layer of the siphuncular tube of later chambers. In his reconstruction, a continuous nacreous layer, which is thin in the earliest part of the siphuncle, underlies the outer chalky layer.

ERBEN, FLAJS & SIEHL (1969: fig. 8; plt. 11, figs. 4, 5) reconstructed the blind beginning of the siphuncular tube as consisting of an outer organic layer and a solid, continuous nacreous wall beneath it. In the explanation of their figure 1 on plate 13, however, they note that the apical portion of this nacreous layer is very rich in organic material. BLIND (1976) found that the outermost hull of the initial cap of the siphuncular tube consists of irregular crystalline elements and of organic sheets, thus confirming both the observations of Mutvei and those of Erben, Flajs and Siehl. Blind stated that the nacreous layer that makes up the apical cap of the siphuncular tube seems to have a prismatic structure. In his figure 3 the wall of the cap is presented as a solid structure that would be impermeable to liquids.

Since the first chamber of *Nautilus pompilius* has been shown to contain gas, this chamber must have been pumped out through the initial part of the siphuncular tube. This seems difficult with a structure as represented by the reconstructions of MUTVEI (1964: text fig. 29), ERBEN, FLAJS & SIEHL (1969: fig. 8) and BLIND (1976: fig. 3). They all show a solidly calcified initial cap the layers of which are continuous with the nacre of the septum. This agrees with Appellöf's assumption that the initial siphuncular tube is solidly mineralized.

However, the layers seen in the cap-like beginning of the siphuncular tube have not all been deposited one immediately after the other; they belong to 2 different phases of secretion (cf. Figure 22). In the first phase, crystal growth starts with the formation of pillar-like crystallites on the nacreous inner wall of the shell apex. Then irregular crystals and sheet-like, discontinuous organic membranes form the chalky layer on the sides of the siphuncle that is now differentiated (Figure 89). Only next to the shell wall purely organic sheets are formed; they cover the porous prismatic layer of the first pillar zone. At the apical margins, growth of irregular crystals and deposition of organic sheets continue when the nacreous septal neck and the septum grow. Thus, the short initial siphuncular tube is very similar to the sections formed later on, with the only exception that the actual horny tube is missing and the nacreous neck is followed by the spongy complex of organic sheets and irregular, loosely packed crystallites. In contrast to later portions, the ending of the organic tube is fused to form the initial cap.

At the end of nacre growth, the first siphuncular tube is functional, and the liquid of the first chamber can be pumped out. When the second chamber forms, a loosely prismatic layer (pillar zone) grows on the sides of the first siphuncular tube, and the new section of the siphuncular tube is fused into the old blind portion. Then a solid calcareous ring forms near the apex of the siphuncular tube. This ring fuses at its apical side and thus becomes a solid prismatic cap that seals the first chamber. In this newly formed, impermeable prismatic cap, the organic layers of the new section of the siphuncular tube are firmly attached. In all other features this second section of the siphuncular tube is like those formed later on.

A pillar zone serving as a fluid reservoir did not exist in the siphuncular system of *Pseudorthoceras* from the Carboniferous period (MUTVEI, 1972a). A spherulitic-prismatic layer (chalky layer) near the septal neck was absent in this form and the prismatic layer on the inner side of the foremost part of the septal neck is solid; there are no pillars or pores. The organic posterior part of the siphuncular tube contains some needle aggregates; it must have been permeable for gas and liquid (MUTVEI, 1972c). As far as we know to date, little space was available in *Pseudorthoceras* for liquids that were not in direct contact with the main body of chamber liquid. This situation would have impeded an extensive vertical mobility.

DENTON (1974: plt. 17) figures the siphuncular tube of the endoceratoid *Dideroceras*. In this animal, the calcareous portion of the siphuncular tube extends into the siphuncular tube formed before, passing halfway through the next older chamber. The permeable part would be confined to the small region lying between the septal neck and the calcareous tube, very much as in the Recent *Spirula*. It is not known whether there were any pillar structures or organic portions as a continuation of the calcareous siphuncular tube, as there are no traces of such formations in this fossil form. But this form shows that among orthocone cephalopods from Paleozoic times, siphuncular structures different from the situation known in *Pseudorthoceras* have existed, which resemble those of the Recent *Spirula*.

Ammonoidea

According to LEHMANN (1976), MUTVEI (1967), ERBEN, FLAJS & SIEHL (1969), ERBEN & REID (1971) and BIRKELUND & HANSEN (1968) the siphuncular tube of the ammonoids has a structure similar to that of *Pseudorthoceras*. Again there is no chalky porous layer, and the posterior part of the siphuncular tube is organic. BIRKELUND & HANSEN (*op. cit.*) think that the structure of the septa

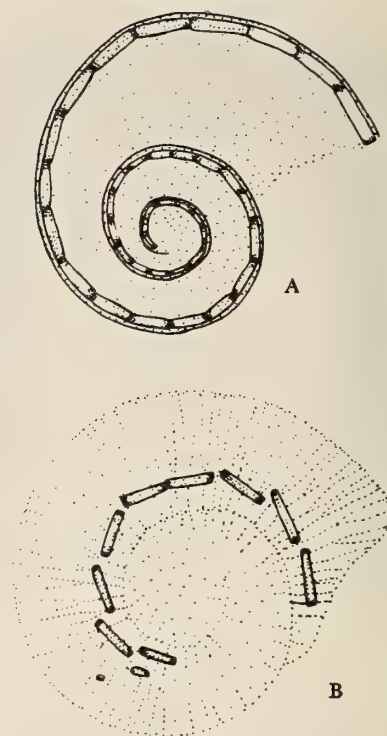


Figure 23

Jurassic ammonoids that had been decalcified before being fossilized in limestone. A: *Glochiceras* with the siphuncular tube in its original position. B: *Subplanites* in which sections of the siphuncular tube have separated and shifted towards the center before the onset of fossilization

and the siphuncular tube described from *Saghahalinites* and *Hypophylloceras* (ammonoids from the upper Cretaceous) indicate that the hydrostatic apparatus of nautiloids and ammonoids are much more similar to each other than MUTVEI (*op. cit.*) suggested, but they do not present any data to demonstrate this.

The siphuncular tube of the Ammonoidea and its attachment to the septum differ in several respects from those of *Nautilus* and *Spirula*.

1. The beginning of the siphuncular tube (caecum) extends into the first ovoid chamber; it is similar to what we have seen in *Spirula*. But this blind ending is hemispherical; the thickness of its wall does not change (BRANCO, 1880; MILLER & UNKLESBAY, 1943; ERBEN, 1962: fig. 1; ERBEN & REID, 1971: plt. 1, fig. 4). This bulbous structure is continuous with

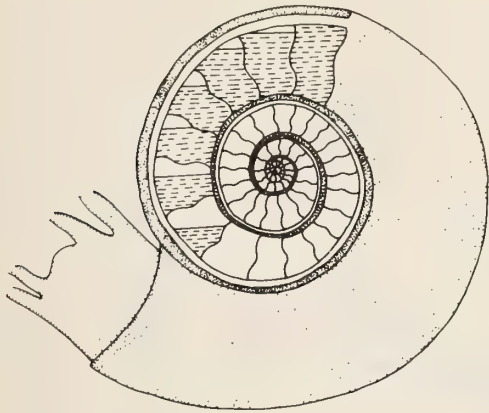


Figure 24

Hypothetical swimming position of an ammonoid, with the presumed distribution of liquid in the last chambers

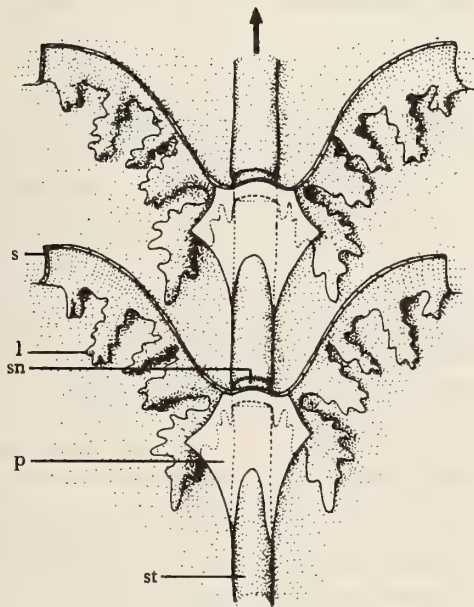


Figure 25

The siphuncular tube (st) of a Jurassic ammonoid, with the septa (s) cut above the folded lobes (l) by which they are attached to the shell wall. The arrow points towards the aperture of the shell. On the apertural part of each section of the siphuncular tube a pellicle (p) or a series of sheets form a cavity apart from the actual chamber. The septal necks (sn) are turned towards the apertural side of the shell

an organic sheet that resembles that observed in *Spirula*; it may also be branched, however (ERBEN, FLAJS & SIEHL, 1969).

2. The structure of the siphuncular tube in the earliest ammonoids reminds one of the tube of nautiloids, for the septal necks are drawn out in the apical direction. But for the majority of late Paleozoic and Mesozoic ammonoids this situation reigns only at early developmental stages (retrosiphonate, retrochoanitic). At the later growth stages, the septa first develop apertural projections where they make contact with the siphuncle, and eventually are entirely drawn out to the apertural side (prosiphonate, prochoanitic) (BRANCO, 1880: plt. 9, fig. 9; MILLER & UNKELSBAY, 1943). Thus the last septal neck of the semi-adult and adult ammonoid always points towards the living chamber (cf. Figure 26).
3. Each portion of the siphuncular tube has the same length as the corresponding chamber (Figure 25). The walls of the tube are not continuous with the septal necks (Figure 26). It has been thought that the siphuncular tube consisted of phosphatic material (ARKELL, 1957; GRANDJEAN, 1910), but recent observations indicate that it is made of organic material similar to the horny tube of the *Nautilus* siphuncle (MUTVEI, 1967; ERBEN, FLAJS & SIEHL, 1969; ERBEN & REID, 1971).
4. The individual portions of the siphuncular tube are not fused with one another, so as to form one continuous organic tube; instead they are connected by calcareous material (MUTVEI, 1967, 1975; BOEHMER, 1936; GRANDJEAN, 1910). Fossil ammonoids (*Subplanites*, *Glochiceras*) from the "Mörsheimer Schichten" (lower Tithonian, upper Jurassic) of the Horstberg near Mörsheim (South Germany) were completely decalcified before they became fossilized (Figures 23a, 23b). Only the outer ornamentation of the shell is found together with the non-calcareous siphuncular tube. Some specimens show this tube in its original dorsal position (Figure 23a); in others it has been shifted to a more central position (Figure 23b). This shifting of the tube must have occurred before the decalcified shells were compacted with the muddy sediment around them. In the original position, the individual tube portions are connected to one another in such a way that the apical part of each tube segment is narrower than the apertural part of the segment formed before (Figure 26). In a decalcified shell not filled with sediment the tube segments may easily have broken apart as soon as the

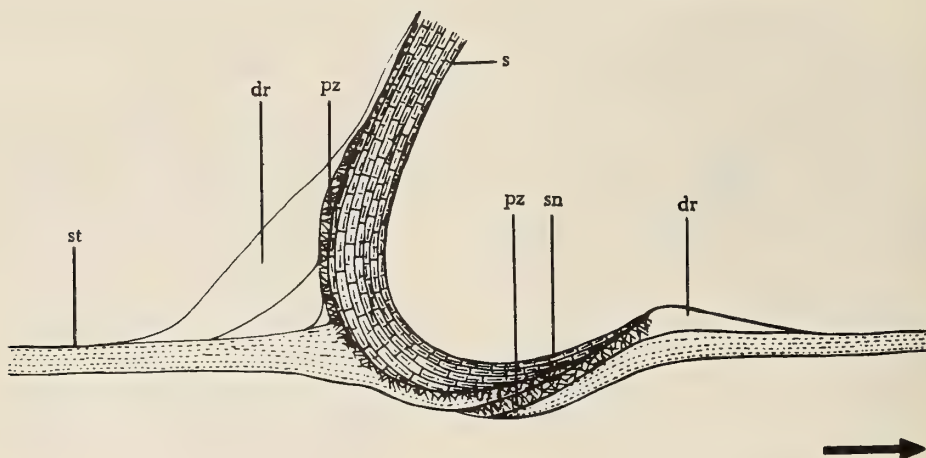


Figure 26

A reconstruction of the septal neck (sn) and the attachment of the siphuncular tube to the septal neck in adult ammonoids. The nacreous septal neck is a continuation of the septum (s). In addition to the de-coupling room (dr) and porous prismatic zone (pz) be-

tween the rear end of a tube section and the septal neck turned towards the aperture of the shell (arrow), each chamber has large de-coupling rooms and a porous zone in the anterior part

calcareous connecting material was dissolved, so that the siphuncular tube was free to shift inside the shell.

5. The descriptions and figures presented by BOEHMER (1836), MILLER & UNKLESBAY (1943), ERBEN, FLAJS & SIEHL (1969) suggest that the organic portion of the siphuncular tube is continuous with the nacreous septal neck as in *Nautilus*, as long as the septal neck points to the apical side. Among the ammonoids, in general, this is only so at very early ontogenetic stages. Representatives of the Paleozoic *Agathiceras* are an exception to this rule in that the septal necks may even increase in length during the individual development until their length is $\frac{2}{3}$ of the chamber length (MILLER & UNKLESBAY, 1943). In this genus we thus find septal necks similar to those of the Recent *Spirula*. The siphuncular tube of juvenile individuals of many Mesozoic ammonoid species has a central or sub-central position. It gradually "migrates" to the outer part of the chamber and becomes marginal by the time when the third volution is reached (cf. ERBEN, FLAJS & SIEHL, 1969: plt. 1).
6. With the change in the orientation of the septal necks during the ontogenesis of most ammonoids the si-

phuncular tube becomes independent of the septum; it can only form after the septum is completed. The nacreous layers of the septal neck are therefore no longer continuous with the horny siphuncular tube. The latter is now attached to the septal neck by secondary calcareous deposits. These may have been porous as in *Nautilus*. Figure 26 is a reconstruction of the attachment of the siphuncular tube to the septal neck of an adult ammonoid. The drawing is based on data presented by MILLER & UNKLESBAY (1943: fig. 6 H; plt. 5, fig. 5) from species of the genera *Eoasianites* and *Perrinites* (both ammonoids from the late Paleozoic), and by GRANDJEAN (1910: fig. 3) and MUTVEI (1967: plt. 14, fig. 2; 1975: fig. 2) from species of the genera *Ludwigia*, *Eleganticeras* and *Promicroceras* from Jurassic strata. In the course of their ontogenesis the ammonoids thus developed an additional porous zone in the siphuncular tube; when the septal necks changed from a retro- to a pro-siphonate arrangement, the chamber liquid could be drained at both ends of the tube segment crossing the chamber.

7. The siphuncular tube of the ammonoids is covered by an organic pellicle that separates from the tube near

its end (BRANCO, 1880; BOEHMER, 1936; ERBEN & REID, 1971; BAYER, 1975). The siphuncular tube is thus attached to the ventral shell wall. What is particularly important is that this pellicle encloses spaces near the end of each tube segment that are not in direct contact with the actual chamber (Figure 25). Liquid could be held there independent of the main body of chamber liquid. The living chamber of different species of ammonoids varies greatly in length, but usually amounts to more than $\frac{1}{2}$ of a whorl (ARKELL, 1957). Thus the position of the last-formed chamber, which is still completely filled with liquid, is different from that of a new chamber in the Recent *Nautilus*. The liquid contents would have been in a position roughly as that shown in Figure 24. This is a situation very different from that shown to exist in *Nautilus* (DENTON & GILPIN-BROWN, 1966).

8. In the majority of the ammonoids, the margins of the septum are corrugated and fluted (Figure 25). Thus many small indentations are formed between the inner face of the outer shell wall and the septum. In chambers only partially filled with liquid this morphological differentiation of the septal sides may have assisted in the de-coupling of the chamber liquid from the liquid contained in the pouches near the end of each segment of the siphuncular tube. This would have an effect similar to what we have seen in the cuttlebone of *Sepia*.

HEPTONSTALL (1970) suggested that the individuals of the genus *Buchiceras*, which in their life have been encrusted with oysters, have been able to maintain neutral buoyancy by removing liquid from the chambers. This author states that in all ammonoids a considerable amount of water would have been kept in the chambers for maintaining neutral buoyancy. Experimental studies by MUTVEI & REYMENT (1973) carried out with plastic shell models confirmed that ammonoid shells in general have been more buoyant than *Nautilus* shells and that in order to maintain neutral buoyancy they must have had more liquid in their chambers. The model presented in our Figure 24 thus probably comes close to reality.

In conclusion we may say that the ammonoids in general have developed a "typical" siphuncular system allowing rapid disposal of the chamber liquid for buoyancy regulation with an effective de-coupling of the main body of chamber liquid from the liquid in closer contact with the siphuncular tissue.

Belemnnoidea

MUTVEI (1971) described the siphuncular tube in representatives of the Aulacocerida and Belemnitida from Jurassic strata. His pictures show that the structure of the pillar zones and the course of the siphuncular tube are strikingly similar to the Recent *Spirula*. The pillar zone extends a little further into the next older siphuncular tube, as it is slightly longer than one chamber. In contrast to *Spirula*, however, the siphuncular tube is organic except for the septal neck.

MUTVEI (1971) thought that the structural features of the belemnite siphuncular tube were neither represented in the Recent *Nautilus* and *Spirula*, nor in any known group of fossil cephalopods. The close relationship that actually exists between the siphuncular tube of *Spirula* and that of the belemnites, in terms of both their structure and functioning (cf. Figure 27), was therefore not yet emphasized by DENTON (1974). Referring to Mutvei's study, Denton suggested that this rather complicated structure might form a connection for liquid movements between one chamber and its neighbours.

MUTVEI (1971) suggested that the aulacocerids and the belemnites had no need for porous layers on the wall of the siphuncular tube and that the whole wall of the tube was permeable. The liquid of the last-formed chamber would thus have been pumped across the 2 organic layers and the "semi-prismatic layer," as Mutvei calls the pillar zone. He comes to the conclusion that belemnites, at least at juvenile stages, could not descend into deep water as *Nautilus* and *Spirula* do.

In contrast to MUTVEI's (1971) statement, but in accordance with his figures 1 and 2 and with his plates, the siphuncular tube of the last-formed chamber in belemnites did not consist of a double-walled organic tube with pillars between the 2 organic layers, but of a single tube the anterior part of which continues into the posterior pillar zone, as in the siphuncular tube of *Spirula*. A double tube can be found only in the second-to-the-last chamber. Considering the situation described from *Spirula* by DENTON & GILPIN-BROWN (1971a), where only the last chamber is filled entirely or to a large extent with liquid, it seems likely that similar conditions existed in the belemnites, *i. e.*, that the wall of the mainly organic tube was largely or entirely impermeable to liquid, so that contact between the chamber liquid and the siphuncular tissue was made through the pillar zone, as in *Spirula*; and that the chambers next to a double siphuncular tube were already empty.

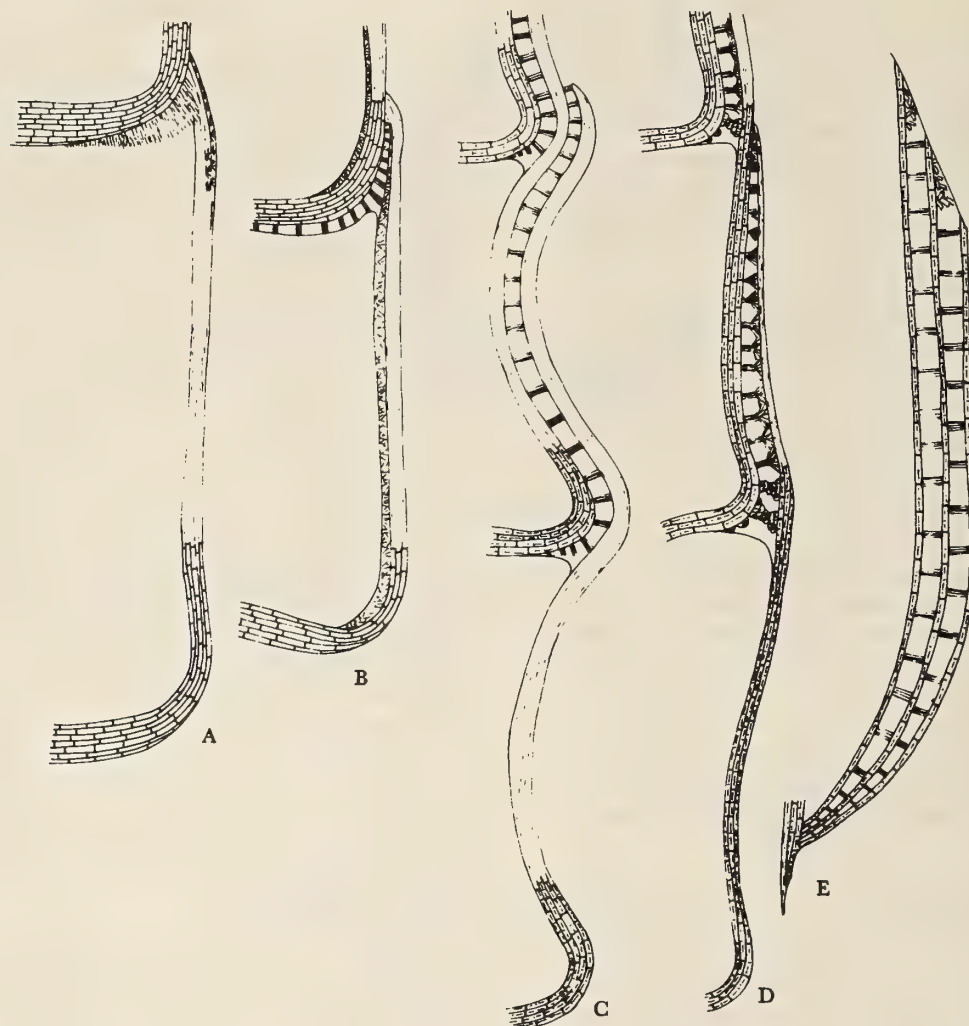


Figure 27

A comparison of the siphuncular systems of fossil and Recent cephalopods. A: *Pseudorthoceras* (redrawn from MUTVEI, 1972).

B: *Nautilus*. C: belemnoids (redrawn and re-interpreted after MUTVEI, 1971). D: *Spirula*. E: *Sepia*. Note the enlargement of the pillar zone from B to E. In *Pseudorthoceras* no pillar zone is found, as in the ammonoids which have developed different

means of de-coupling liquid from the main body of chamber liquid. In *Nautilus* the pillar zone is small in comparison to the chamber volume. In the belemnites and in *Spirula*, the pillar zone is enlarged, but still chambers of considerable volume are present. In *Sepia* finally the pillar zone alone remains and fulfills the chamber function.

Spirula is known to make extensive vertical migrations; it lives mainly below 200 m, but usually does not descend deeper than 1000 m. CLARKE (1970) showed that during the day *Spirula* stays at depths around 600 - 700 m. Since the siphuncular tube of the belemnites appears to be rather strong, a vertical mobility similar to that of *Spirula*

can be presumed. The pillar zone represents a large space for liquid, apart from the main body of liquid in newly formed chambers, so that high osmotic pressures may have been established, enabling the belemnites to maintain neutral buoyancy at great depths.

CONCLUSIONS ON THE PHYLOGENETIC DEVELOPMENT OF THE SIPHUNCULAR SYSTEM

The siphuncular system of the only living cephalopods that have a chambered shell is a very conservative structure. This undeniable fact is partly obscured by the differences in the gross morphology of the shells and their respective siphuncular systems in *Nautilus*, *Spirula* and *Sepia*.

As we have seen that the structural elements of these 3 modifications of a common type of siphuncular system are very similar, it remains to be seen whether their formation is also similarly timed with the formation of a new chamber.

MUTVEI (1972a) assumed that in *Nautilus* the lamellar pillars ("prismatic layer") on the apertural side of the septum are formed as the final layer of a new septum before secretion of calcareous material ceases. It seems more likely, however, that the pillars are formed just before the pellicle that will cover them is secreted, and that these 2 steps initiate the withdrawal of the mantle, which is accompanied by secretion of body fluid into the new chamber now forming. In the "state of rest," the epithelium of the mantle would thus closely join the smooth surface of nacre. In chronological terms, formation of pillars would thus be the earliest of the events in the formation of a new chamber, similar to the sequence found in *Spirula* and *Sepia*.

In *Nautilus*, the structure of the pillars is transitional to the columnar structures that are formed by nacre platelets piled up to pyramid-like complexes (MUTVEI, 1972a) (Figures 93, 94). It is conceivable that such pillars have existed in the Paleozoic orthocone cephalopods, between the walls of successive calcareous siphuncular tubes (cf. DENTON, 1974: pl. 17).

In the belemnites (MUTVEI, 1971) and in *Spirula*, the lamellar pillars are consistent with the lamellar structure, not with the nacreous structure. During the evolution of the endocochleate shell, the nacreous layer must have been transformed into the lamellar layer. To our knowledge, all ectocochleate cephalopods show only a nacreous structure. Structures transitional between nacreous and lamellar are present, however, in the septal neck of *Nautilus* and *Pseudorthoceras* (MUTVEI, 1972a, 1972c).

Spirula and the belemnites have a wide zone of the siphuncular tube occupied by the pillars. This pillar zone is distinct from the actual chamber. In *Sepia*, however, the actual chamber is lost, and the pillar zone is opened up into a broad blade. The organic sheets, confined to the anterior part of the pillar zone in *Spirula*, now extend

throughout the "chambers" of the cuttlebone. No significant difference has been found between the structure of the lamellar pillars of *Spirula* and those of *Sepia*. Also the septa of *Sepia* and the anterior siphuncular tube of *Spirula* show the same composition of their lamellar structure.

The cuttlebone can withstand high external pressure. *Sepia officinalis* is known to live in coastal waters and to descend to a depth of about 150 m. DENTON (1974) has shown that cuttlebones of *Sepia officinalis* implode at pressures around 20 atmospheres, which corresponds to a depth of about 200 m. Other species of *Sepia* live at greater depths, however. *Sepia elegans* and *S. orbignyana* have been found on bottoms as deep as 450 m (cf. MANGOLD-WIRZ, 1963). It is not surprising then that the strong shell of *Nautilus* can withstand pressures of 60 to 70 atmospheres (DENTON & GILPIN-BROWN, 1966), but the rather more delicate shell of *Spirula* regularly withstands pressures twice as high, and occasionally pressures corresponding to depths of more than 2000 m (DENTON & GILPIN-BROWN, 1971a).

Since the structure of the siphuncular tube of the ammonoids and belemnoids known to date resembles so much the structures in *Nautilus* and *Spirula*, it seems reasonable to assume that these fossil cephalopods were able to descend into deep waters.

DISCUSSION

The only cephalopod with a chambered shell of which we know the embryonic development is *Sepia*. Although this particular development cannot be taken as representative in every detail for other cephalopods, Recent or fossil, that have a calcified, chambered shell, it is at any rate interesting to consider very carefully all the features of *Sepia* embryos that might present signs of ancestral features.

Setting aside the question of whether or not the closure of the shell sac in the embryo of Recent Coleoidea is a recapitulation of the process by which the external shell of ectocochleate cephalopods has been surrounded by the pallial integument to become the internal shell of the endocochleate type, one wonders what the phenomena of folding and stretching of the shell sac epithelium at the early stages of shell formation in *Sepia* embryos signify.

One wonders whether these phenomena are related to the formation of the so-called "cicatrix" in the shell of the Recent *Nautilus* and of certain fossil Nautiloidea. The morphological features of the *Sepia* protoconch closely match the definition of the cicatrix as given by ERBEN & FLAJS (1976). The presence of such a structure in the

protoconch cannot be taken, however, as an indication of the presence or absence of a post-embryonic larval phase.

Considering the morphological relationship of the fins to the shell complex, one may formulate several hypotheses on the origin of these special locomotory organs. For example, it is conceivable that the cephalopod fins are derived from originally larval "appendages" that already served locomotion. This hypothesis could lead to the construction of a larva that had some similarity with a typical veliger, but in which the locomotory appendages (equipped with cilia) were part of the pallial complex, in contrast to the cephalic vela.

If some or all ammonoids had true larvae, these larvae may have been anything but veligers of, e. g., a gastropod-like appearance as figured by ERBEN (1964) (cf. also JÄGERSTEN, 1972).

Before one attempts to interpret the sequence of calcareous formations deposited on the early organic shell of *Sepia*, one must of course be certain that the steps considered are well distinguished. Looking through the literature, one finds a great deal of contradiction and confusion as to the first appearance of certain shell structures. Thus KOELLIKER (1844) correctly stated that the first embryonic shell of *Sepia* is not mineralized. APPELLÖF (1893) doubted that these observations were correct, as he had found only calcified shells in the embryos he dissected. Koelliker also correctly observed that in the earliest embryonic chambers of the cuttlebone, the pillars are more regularly columnar than in the later chambers, whereas Appellöf made no differentiation between the pillars of the earliest and those of the later chambers.

However, APPELLÖF (1893) correctly stated that the fork is not yet formed in the embryonic cuttlebone, whereas NAEF (1928) was convinced he saw the fork layer corresponding to each embryonic chamber. SPIESS (1972) also thought that all parts, including the spine, were well differentiated in the embryonic cuttlebone, but he found no horizontal organic sheets in the embryonic chambers. These are present, however, whereas the spine begins to form only towards the end of embryonic development in *Sepia officinalis*. If the fork and the spine were ancestral features, one would indeed expect to find them among the earlier differentiations of the shell.

As we do not yet know the embryonic development of *Spirula*, we are again restricted to hypotheses. These will necessarily be misleading if the structural properties of the initial chambers are not considered in every detail.

Although APPELLÖF's (1893) idea of the formation of the first chamber of *Spirula* was hampered by his assumption that this chamber is originally filled with soft chitin, his description of the first chamber is correct. NAEF (1928), however, saw a double-layered structure in the

outer wall of the first chamber, and a rudimentary septum continuous with the septal neck. But the ridge-like constriction of the inner apertural wall of the first chamber has no structural similarity with the actual septa, and it is not continuous with the septal neck. Furthermore, NAEF (*op. cit.*) noted a feeble calcification of the "prosipho," and he mentions a transversal supporting rod ("Sagittallamelle") lying between the "prosipho" and the ventral chamber wall (NAEF, *op. cit.*: text fig. 279a). Such an additional lamella does not exist, and the "prosipho" sheet shows no trace of calcification.

The morphology and the fine structure of the first chamber in *Spirula*, with its blindly ending siphuncular tube, is very similar to the first chamber of ammonoids with the so-called caecum. A comparison of the first chamber of *Spirula*, opened up (Figure 64), and the first chamber of the ammonoid *Eleganticeras* (LEHMANN, 1976) will show this. SCHINDEWOLF (1933) suggested that a caecum of the type known from *Spirula* and the ammonoids represents the primitive situation, and that the siphuncular end as it now exists in the first chamber of *Nautilus* is the result of a secondary differentiation.

The shell structure of the first chamber (ERBEN, FLAJS & SIEHL, 1968, 1969; KULICKI, 1975) and of the prosepium and flange in ammonoids also shows great similarity between different ammonoid species on the one hand, and *Spirula* on the other. There is one important difference, however, in that *Spirula* shows a constriction between the first and second chamber that is much stronger than subsequent ones, whereas the ammonoid shell presents an even spiral growth from the beginning. Only in some ammonoideans of the early Devonian age, when the coiling of the first whorl was still evolute, as it is in *Spirula*, a constriction reminiscent of the early *Spirula* shell has been observed (ERBEN, 1964); a similar feature has also been noted in longicone nautiloids (SCHINDEWOLF, 1933).

In the literature we find two opinions as to the development of the first septum in the ammonoids. One is based on the observations of ERBEN (1964) and ERBEN *et al.* (1968, 1969); it claims a free larval life for the young. The other is expressed by BIRKELUND & HANSEN (1968, 1974), DRUSHITS & KHIAMI (1970), and by KULICKI (1974, 1975); it suggests that the ammonoids had a direct development, corresponding to what is known of all the Recent coleoid cephalopods so far studied (cf. BOLETZKY, 1974b).

In the first theory, three phases similar to those of gastropod and lamellibranch metamorphosis are postulated. In the first phase, the early embryonic shell gland produces a shallow, bowl-shaped protoconch or a simple organic cap. This early formation is enlarged until a shell of nearly one complete whorl is formed. With this

shell, the animal hatches as a larva similar to a praeveliger or trochophora. In the shell, this stage would be marked by a constriction and a condensation of growth lines.

In the second phase, a free swimming, planktonic veliger or veliger-like larva adds shell material to the aperture in such a way that a ventral indentation forms, reflecting the ventral position of the velum. The secondary walls of the embryonic shell are then added. Only shortly before the end of the larval phase, the "flange" and the "proseptum" are formed (the flange is the first prismatic addition to the ventral inner side of the shell; the proseptum is the constriction of the aperture of the first chamber). The siphuncle now differentiates.

The end of metamorphosis and the beginning of the third phase is documented by the so-called nepionic constriction, a distinct mark in the shell wall; the prismatic shell layers wedge out, or the direction of their growth is suddenly inverted, apparently due to a temporary retreat of the mantle edge. The first nacreous layers are formed and the buoyancy apparatus becomes functional with the formation of the first primary septum that closes the second chamber. This first septum may have a prismatic (ERBEN, FLAJS & SIEHL, 1968, 1969) or a nacreous structure (BIRKELUND & HANSEN, 1974; KULICKI, 1975).

The second theory was formulated by KULICKI (1974, 1975). According to this theory, the embryo first forms a cup-shaped prismatic shell, the aperture of which is then reduced by the addition of shell material on the ventral inner side, which forms the flange. Immediately after this, another constriction (proseptum) is formed next to the flange. During further growth, the soft tissue filling the initial chamber is withdrawn, and the epithelium separates from the wall of the first embryonic shell. Only a minute part of it remains attached at the end of what will become the "prosiphon" (organic sheet between the end of the siphuncular tube and the chamber wall). Along with this, the wall of the proseptum grows to become an annular constriction (as a continuation of the initial ventral ridge in front of the flange that is also ventral). After the proseptum, the prosiphon and the caecum take shape as soon as the tissue is withdrawn from the first chamber. In the ammonoid genus *Quenstedtoceras*, a newly hatched animal would have 3 complete chambers, if the nepionic constriction marks the stage of shell growth reached at hatching. TRUEMAN (1940) reports on shells with 3 septa and a diameter of 0.5 to 0.6 mm, which he considers to be the shells of newly hatched *Arnioceras*.

In *Spirula*, the construction of the shell wall has been described in different ways (cf. DAUPHIN, 1976). APPELLOF (1893) noted 2 layers, the inner primary and the

outer secondary. BØGGILD (1930) found that the inner shell wall consists of regular prisms, whereas the outer part would be homogeneous. It is very likely that Bøggild observed the layers of the primary wall only. MUTVEI (1964a) stated that a periostracum is not known from the *Spirula* shell. NAEF (1928) gave a description that comes close to the actual structure of the *Spirula* shell. He found 3 layers, of which the thickest is the middle layer that consists, according to him, of a somewhat irregular nacre (lamellar layer!). Our observations make it clear that a lamellar layer makes up the bulk of the shell wall, with an underlying prismatic layer. This innermost layer shows only the structure that was thought to compose the entire primary wall, according to Mutvei's description. If the central layer with its lamellar structure is considered to be similar to the nacreous layer of *Nautilus*, the shell wall of *Spirula* certainly appears very similar to the wall of the *Nautilus* shell. In contrast to Mutvei's assumption that the superior part of the epithelium lining the "living chamber" of *Spirula* can produce only prismatic layers (outer wall), whereas the posterior parts produce 4 different layers of the septum and the siphuncular tube, we can now state that the epithelium lining the "living chamber" can produce similar aragonitic deposits independent of their position in the chamber.

In his analysis of the *Spirula* shell, MUTVEI (1964a) found that the septal and siphuncular deposits retained their original structure, being made up of the same 4 layers as the shell of *Nautilus*. Mutvei observed that these 4 layers are visible in the newly formed siphuncular tube only; in the posterior part of the tube which he thought is formed later, these deposits are reduced and consist of a single layer, the spherulitic-prismatic layer. In Mutvei's view, the posterior parts of the siphuncular tube of *Spirula* are at an advanced stage of reduction as compared to the corresponding formations of *Nautilus*. The septum and the anterior part of the siphuncular tube are assumed to be made of an outer conchiolin layer (organic layer), a spherulitic-prismatic layer, a nacreous layer, and an inner semi-prismatic layer. We can not confirm these observations of Mutvei. Depending on the part of the shell, one finds different sequences of layers (cf. Figure 7).

In a diagrammatic presentation of the shell and its epithelium, MUTVEI (1964: text fig. 28) figures a newly formed septum with the epithelium and the siphuncular tube that extends through $1\frac{1}{2}$ chambers. On the anterior part of the siphuncular tube, which has just been formed, pillars are present. Mutvei states that the semi-prismatic layer (pillar zone; "Pfeilerchen" of Appellöf) forms a continuous coat on the ventral face of each septum and that it also invests the inner face of the siphuncular tube. Our observations indicate that this reconstruction is er-

roneous, as the pillars in fact are formed along with a new septum and anterior part of the siphuncular tube.

APPELLÖF (1893) described the annulations of the pillars and the organic sheets between the anterior pillars in *Spirula* and compared them to the corresponding structures of the *Sepia* shell. He also noted the coarse structure of the pillar apices, especially near the posterior end of the pillar zone, where pillars and needle aggregates are interlaced, and he compared this area with the posterior part of the siphuncular area in *Sepia*, where crystal aggregates are also present. These very clear similarities were not recognized by NAEF (1928) who differentiated between a calcareous tube ("Kalkdüte"), into which an organic tube ("Conchindüte") were fitted.

The lamellar structure that forms, according to MUTVEI (1964a, 1964b, 1970), the type of nacre found in belemnoids and in *Spirula* differs in one important point from the nacre of gastropods, pelecypods and of *Nautilus*. In the lamellar layers, there are no concrete tabular plates of a certain size that is characteristic of each shell section, because the small components of each platelet may vary in size. Interlamellar partitions of organic shell material are not distinct in the lamellar layers, so that they do not present, in a section, the appearance of brickwork or stacks of coins that is so typical of nacre. Although the lamellar structure may have developed from the nacreous structure, or vice versa, they are clearly distinct structures. This is also indicated by the different composition of the organic septal material in *Nautilus* and in *Spirula* (GRÉGOIRE, 1961, 1962).

DENTON & GILPIN-BROWN (1961b) showed that the oldest (embryonic and early post-embryonic) chambers of the *Sepia* shell are almost completely filled with liquid at the adult stage. These authors found that nevertheless these oldest chambers can again be pumped out. In large individuals of *Sepia officinalis* and *S. orbignyana*, the siphuncular zone of the oldest chambers is often covered with a secondary calcareous deposit. When this is present, the respective chambers can probably no longer be pumped out by the siphuncular epithelium. In *Sepia pharaonis*, younger individuals already show this kind of mineral cover on the siphuncular zone of the oldest chambers, with an additional lamellar, mainly organic deposit uppermost (Figure 4). Thus, the oldest chambers, which are refilled with liquid, are completely sealed up.

Although we know very little of the function at the cellular level of the different parts of the shell sac epithelium, it is clear that the epithelium of the siphuncular zone fulfills very different tasks, according to the different phases of shell formation. It first takes a part in the formation of the chamber layers, then acts as a "pumping organ" when the chamber is emptied, and finally part of

it secretes the calcareous and organic components of these last shell deposits on the ventral side of the cuttlebone. The great change in the histological aspect of the epithelium during the first two steps has been described by DENTON & GILPIN-BROWN (1961a).

Finally, it can be conjectured that the secondary calcareous deposits on the posterior part of the siphuncular zone of the *Sepia* shell correspond to the intra-siphuncular deposits that are observed in many Paleozoic cephalopod shells. Deposits that are not calcareous, however, are found in the siphuncular tube of the first chamber of *Spirula* (Figure 66), and also in the first-formed parts of the siphuncular tube of *Nautilus*. These translucent organic deposits completely fill the tube so that the siphuncular tissue is no longer in contact with the first chambers.

SUMMARY

1. The structural composition of the shell is essentially alike in *Sepia* and *Spirula*, notwithstanding their very dissimilar form. The lamellar structure composes the septa and the greater part of the wall in the cuttlebone and in the *Spirula* shell. The inner prismatic layer of the *Spirula* shell is homologous to the inner layer of the *Sepia* shell. The external spherulitic-prismatic layer that is produced by the secondary shell epithelium is alike in both types of shell.
2. The early embryonic shell or protoconch of *Sepia* is different from that of *Spirula*. The former shows similarities to the protoconch of *Nautilus* and many fossil Nautiloidea, whereas the shape and composition of the early *Spirula* shell resemble very much that of the Ammonoidea and Belemnoida, including the first prismatic apertural constriction (proseptum) and the end of the siphuncular tube (caecum) with its sheet-like extension that is fixed to the shell wall. *Sepia* and *Nautilus* both show a groove in the initial organic shell cap, the so-called cicatrix. The similarity of these structures suggests an identical configuration of the respective parts of the primary epithelium. So far, the embryonic development of *Sepia* only is known.
3. The lamellar structure is composed of 0.1 - 0.3 μm units, similar to the composition of other biocrystal structures of higher organisation known from the molluscs: nacre, crossed lamellae and the helical structure. Like the closely related nacreous structure, the lamellar structure is elaborated in gelatinous lamellae that have the same thickness as the crystalline lamellae.
4. The siphuncular system is essentially alike in *Sepia* and *Spirula*, as the so-called chambers of the cuttlebone

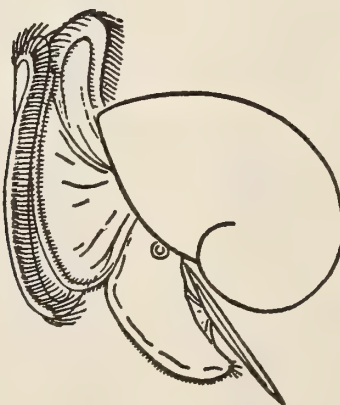
represent the siphuncular system and septal necks of the *Spirula* shell. The actual chamber of *Spirula* is not represented in the *Sepia* shell. The septal neck (lamellar structure) of *Spirula* is homologous to the septum of *Sepia*, and the pillars of the siphuncular wall of *Spirula* are homologous to the chamber pillars of the cuttlebone. The irregular crystals and crystal aggregates in the posterior part of the siphuncular zone of each cuttlebone chamber are homologous to the very similar structures found in the posterior part of the siphuncular tube in *Spirula*.

5. The function of the siphuncular system has probably never changed in the chambered shells of cephalopods. With the suppression of the actual chamber in the *Sepia* shell, the "main body of liquid," which in the chambers of other shells is "de-coupled" from the small part of liquid in contact with the siphuncular wall, is no longer a distinct component of the buoyancy apparatus; rather the innermost parts of the cuttlebone chambers are fluid reservoirs that are **analogous** to the actual chamber as a reservoir.

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First Record of *Okenia impexa* Marcus, 1957 from the Western Atlantic in the Mediterranean

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(1 Plate; 2 Text figures)

INTRODUCTION

During a study of the Nudibranchia of the western Mediterranean, we collected 2 rare species at Naples and at Banyuls: *Okenia mediterranea* (von Ihering, 1886), which has not been mentioned since Ihering, and *O. impexa* Marcus, 1957, from São Paulo and North Carolina. Because there are some consistent differences between the Mediterranean and the western Atlantic material, the anatomy of the Mediterranean *O. impexa* is described here. We hope that on the basis of this description further research in the western Atlantic will help to decide whether the species has entered recently into the Mediterranean or whether it is a geographical subspecies.

GONIODORIDIDAE

Eudoridacea suctoria, phanerobranchiate, rhinophores laminated without sheaths. There is a narrow pallial ridge on the head and on the sides, with or without simple appendages – or the pallial ridge is reduced and there are only appendages. Radula without median tooth, often with 2 lateral teeth, the inner one hook-shaped and larger than the often plate-shaped marginal tooth. Labial cuticle smooth or armed with hooklets or plates.

Okenia Menke, 1830

Body with a narrow pallial ridge with simple appendages. The anterior border of the notum is developed as a narrow, sometimes bilobed frontal velum. Rhinophores often laminated only behind. Gills often unipinnate. Radula formula 1 · 1 · 0 · 1 · 1. First lateral tooth large and hook-shaped with a smooth or denticulated inner border. Outer lateral tooth small, plate-shaped with 1, 2 or 3 cusps. Labial cuticle smooth or armed with hooklets or plates. Penis armed with cuticular spines.

Okenia Menke, 1830 (on official list no. 1995, Bull. Zool. Nomencl. 1974: 13). Type species: *Idalia elegans* Leuckart, 1828 (Figure 2). MENKE, Synopsis methodica molluscorum generum omnium 1830: 10. For discussion see: BERGH, 1881: 144; 1907; BURN, 1971: 151; LEMCHE, 1971: 262 - 266; MARCUS, 1957: 434 ff.; MARCUS & MARCUS, 1967: 203.

I agree with MARCUS (1957: 436) and BURN (1971: 151), that the division made by BERGH (1881: 144) into the subgenera *Okenia* s. str. (Bergh: *Idalia* s. str.) (with appendages in the middle of the back) and *Idaliella* (without such appendages) is not natural.

Okenia impexa Marcus, 1957

(Figures 1a, 1b, 4, 5)

Material: Banyuls: 5 specimens, alive, 3 - 4 mm length, 1 - 20 September 1976; on *Halimeda* and Corallinaceae, 15 m near Cap Oullestreil and 5 m near Collioure. Naples: 2 specimens, 3 - 4 mm length, 11 March 1977, 7 m, sand.

Description: Description of an undamaged animal found on *Halimeda* in 12 - 15 m depth in front of Cap Oullestreil, 14 September 1976. The genital organs and the radula of a 2nd specimen of the same length are described.

Alive and extended, the body is 4 mm long with a maximum height and width of 0.8 mm. The notum is not broader than the foot and is bordered frontally and laterally by a distinct pallial ridge. Caudally the notum merges without pallial ridge into the 1.5 mm long tail. Around the head, the pallial ridge bears 6 digitiform, apically pointed, rather stiff appendages (another specimen has only 4, a 3rd one, 5 appendages), the 4 anteriormost of which are about 1 mm long, and longer than both lateral ones. Behind the rhinophores the pallial ridge has 5 cerata on each side, the last 2 are united at their bases. From cephal to caudal, these lateral cerata increase to a length of 0.8 mm. They have a characteristic shape, swell-

ed and rounded at the tip, but extremely narrowed at the base. Halfway between the rhinophores and gills a low longitudinal median cresta begins, which ends at the gills. It bears one short, finger-shaped, pointed tubercle in front of the gills. The rest of the notum is smooth without any tubercles. The 0.8 mm wide foot possesses short, 0.1 mm long, protruding and pointed front angles and is pointed behind. The smooth anterior border of the foot is neither horizontally grooved nor medianly notched.

The head is covered by a small bilobed veil, only slightly set off from the head on the sides.

Extended, the rhinophores have a length of 1.2 mm with a maximum diameter of 0.2 mm. They are smooth in front and laminated with 10 leaflets behind only, from the tip almost to the base.

Four simple pinnate gills, which have a maximum length of 0.8 mm, insert tightly around the anus, which is situated 2.2 mm from the anterior border of the body.

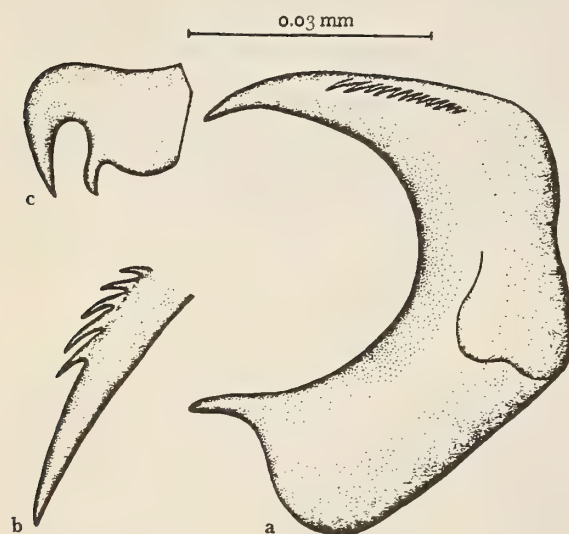


Figure 4

Okenia impexa

Radula: (a) 1st lateral tooth - (b) denticulated inner border of the 1st lateral tooth - (c) marginal tooth

The genital openings are situated somewhat behind the rhinophores and closely below the right pallial ridge.

The labial armature consists of a thin cuticular ring without recognizable papillae.

The radular formula (Figure 4) of an animal of 4 mm is $15 \times 1 \cdot 1 \cdot 0 \cdot 1 \cdot 1$. The radula rhachis shows no cuticular support. The 1st lateral tooth is strongly hook-shaped and twice as long as the plate-shaped marginal tooth. Basis (0.06 mm) and tip (0.05 mm) of the 1st lateral tooth stand in a more or less straight angle towards one another. Its tip bears on the inner border about 10 pointed denticles, which decrease from the tip towards the basis. The marginal tooth is 0.027 mm high and 0.018 mm wide. It possesses a sharp cusp and its edge has one hook-shaped denticle.

The specimens of 3 and 4 mm body-length copulated. Nevertheless, no egg masses could be observed. One day after copulation, the genital organs of a 4 mm long animal were studied (Figure 5). The hermaphrodite duct enters into a wide ellipsoid ampulla. The postampullar hermaphrodite duct is enclosed by the well-developed, swollen female gland mass in such a way that its proper course can not be pursued. Immediately behind the bifurcation of the spermooviduct, the vas deferens increases to a long, big prostatic tube, which encloses the ampulla. The prostate occupies about $\frac{2}{3}$ of the length of the vas deferens. It continues into a short ductus ejaculatorius, which ends in a penis, armed with pointed cuticular spines. The sheath of the penis closely encloses the penis. Between the sheath of the penis and the vagina a gland is situated, which appears white, compact and grape-like after fixation. The vagina is a straight duct, which runs beside the penis into a common vestibulum. At the wide vaginal duct a spherical bursa and an ellipsoid receptaculum insert close to one another. Both vesicles appear to have a short stalk. Nevertheless, their mode of insertion could not be clearly established because of their tight filling.

The general body colour is a bright transparent whitish yellow. The rhinophores, the gills and the cerata as well as the pallial ridge and the median cresta show, almost uniformly, this transparent yellow. On the notum and the sides of the foot there is a dense, fine brown (in

Explanation of Figures 1 to 3

Figures 1a, 1b: *Okenia impexa* Marcus, 1957 4 mm

Figure 2: *Okenia elegans* (Leuckart, 1828) (Banyuls) 5 mm

Figures 3a, 3b, 3c: *Okenia mediterranea* (von Ihering, 1886)

4 mm

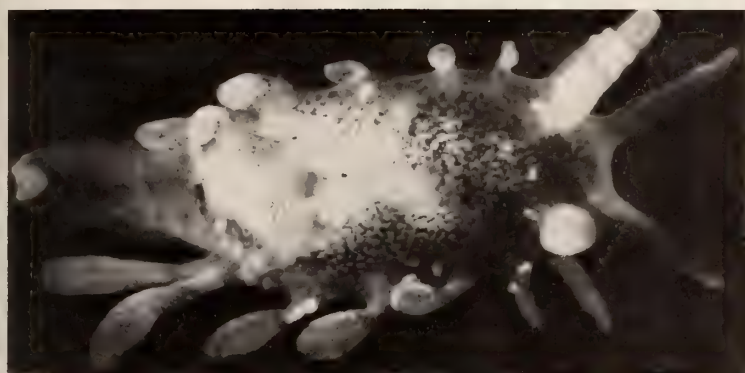


Figure 1a



Figure 1b



Figure 2



Figure 3a



Figure 3b



Figure 3c



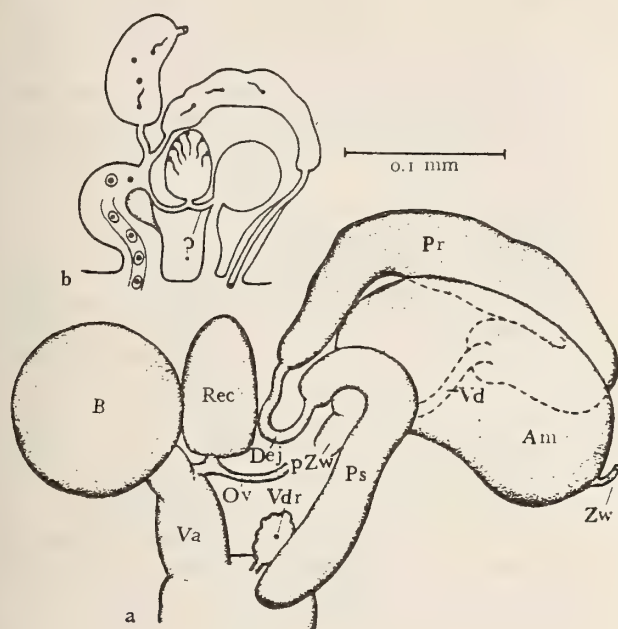


Figure 5

Okenia impexa

Reproductive system: (a) anatomy - (b) schematic
 Am - ampulla B - bursa D. ej. - ductus ejaculatorius
 Ov - oviduct Pr - prostate Rec - receptaculum seminis
 Va - vagina Vdr - vestibulum gland

artificial light red-brown) punctation, which is the most distinct on head and back, the most weak on velum and tail. The sides of the body show an average brown pigmentation. Moreover, some few brown dots are situated basally on rhinophores, gills and cerata. All opaque white pattern is lacking. The eyes and spiculae may be observed through the epithelium.

DISCUSSION

MARCUS (1957) published a list of 15 known species of *Okenia*, and 2 new ones, thus altogether 17 species. Since then, the following species - as far as I know - have been described:

Okenia opuntia Baba, 1960: 80; Japan
Okenia plana Baba, 1960: 80; Japan

Okenia babai Hamatani, 1961: 117; Japan
Okenia angelensis Lance, 1966: 76; north-eastern Pacific
Okenia mija Burn, 1967: 55; south-eastern Australia
Okenia sapelona Marcus & Marcus, 1967: 203; south-eastern coast of the United States
Okenia cupella (Vogel & Schultz, 1970: 390; eastern coast of the United States) (*Cargo* Vogel & Schultz, 1970 is a later subjective synonym of *Okenia*; cf. BURN, 1971 and Opinion 1014, Bull. Zool. Nomencl. 1974)
Okenia ascidicola Morse, 1972: 92; Massachusetts

The external appearance of *Okenia impexa* Marcus, 1957 differs clearly from most of the above mentioned species because of its peculiar cerata, which are swollen and rounded at the tip, narrow at the base, and also because it possesses a single median tubercle on the back. Comparably shaped cerata and 1 median appendage are possessed - among the above mentioned 25 species - only by *O. plebeia* Bergh, 1902 with a rounded lateral tooth and plate-shaped elements on the labial cuticle (BERGH, 1902: plt. III, fig. 17) and *O. impexa* Marcus, 1957. After the examination of the Mediterranean specimen, Dr. Eveline du Bois-Reymond Marcus confirmed that our animals are *O. impexa* Marcus, 1957. The shape of the radula, the labial armature and the genital complex correspond in the main features in the animals from the western and from the eastern Atlantic. But there are some differences in the internal anatomy, e. g., in the shape of the lateral tooth, which has 2 cusps in the Mediterranean (Figure 4c), 3 cusps in the western Atlantic specimens. The external habitus also shows differences. In the western Atlantic specimens the median ceras of the notum is club-shaped and is of the same length as the appendages of the notum border. All the specimens from Naples and Banyuls however, have a very short, pointed, finger-shaped tubercle (Figure 1b). The lateral posterior appendages of the notum border are apically swollen and rounded in the Mediterranean animals (Figures 1a, 1b), "claviform though pointed" (MARCUS, 1957: 434) in the western Atlantic specimens. Because we only know very little about the variability of the species in the western Atlantic (MARCUS, 1957, 1961) and in the Mediterranean, we cannot decide whether the mentioned differences are within the normal range of variability of the species or whether they are a manifestation of an independent development in the western and eastern Atlantic and, thus, whether or not the 2 forms represent 2 geographical subspecies. If further observations in the western Atlantic confirm the constancy of the above mentioned geographical differences, I name the eastern Atlantic subspecies *Okenia impexa banyulensis*. But as the species was not

found in Naples or Banyuls prior to 1976, it may be possible that *Okenia impexa* has only recently entered into the Mediterranean, similarly as, presumably, *Doto doerga* Marcus & Marcus, 1963 (SCHMEKEL, 1958).

Should further research establish that this is indeed a new subspecies, I select the specimen described as the holotype (Figures 1a, 1b) and the dissected specimen as paratype. The holotype has been deposited in the collection of the Naturhistorisches Museum in Basel, Switzerland; the dissected material in the form of microscope slides is on deposit at Münster, Germany.

Okenia mediterranea (von Ihering, 1886)

(Figures 3a, 3b, 3c)

Material: Naples: 3 specimens, alive, 3–5 mm long, from *Posidonia* and other dredged material. Canale di Procida, 20 m, 19 August 1963; Bocca piccola, 75 m, 12 November 1964; Banco Capo Miseno, 30 m, 23 March 1967.

Description: Description of a live 4.5 mm long animal, found 19 August 1963 on *Posidonia*, Canale di Procida, 20 m.

Without measuring the cerata, the flat body (Figure 3) has a length of 4 mm after fixation. The notum has – also without the cerata – its maximum width of 1.6 mm immediately behind the rhinophores. The maximum height of 1.2 mm is found in the region of the pericard in front of the gills. The notum is broader than the foot and is anteriorly and laterally bordered by an approximately 0.5 mm broad free notum margin. Caudally the notum merges without pallial ridge into the weakly keeled tail, measuring about $\frac{1}{3}$ of the body length. The free notum border bears finger-shaped pointed appendages. On each side are situated 8 cerata, the last 2 of which are united at their base. One unpaired ceras is situated medianly behind the gills. The longest, 1 mm long cerata insert in the middle of the anterior pallial ridge; caudally the appendages become continually shorter. In the median line of the notum a low keel-shaped cresta runs from the rhinophores towards the gills. It shows 5 small elevations, but it does not bear tubercles. The rest of the notum is smooth. The smooth anterior border of the foot possesses rounded front angles. Frontally the foot has its maximum width of nearly 1 mm, which decreases continuously towards the tip of the tail.

A bilobed veil is situated over the mouth and underneath the notum border. This veil has large rounded lobes of 1.2×0.4 mm (Figure 3b) and a median emargination.

The very slender, 1.2 mm long rhinophores are situated 0.4 mm from the anterior border of the notum. They are smooth in front and laminated with about 23 fine lamellae only behind, from the tip almost to the base.

Five slender, unipinnate gills, which have a maximum length of 1 mm, are situated medianly at the beginning of last body-third. They insert on a wide, open half-circle in front of the anus.

The genital openings are situated at the end of the 1st body-third closely below the right notum ridge.

The labial armature consists of a cuticle ring, which is bordered by closely set, low, denticulated papillae on $\frac{1}{4}$ of its circumference.

The radular formula of a 5 mm long live animal is $18 \times 1 \cdot 1 \cdot 0 \cdot 1 \cdot 1$. The radular rhachis bears no teeth and shows no cuticular support. The 1st lateral tooth is hook-shaped and twice as long as the plate-shaped marginal tooth. Basis (0.075 mm) and tip (0.06 mm) of the 1st lateral tooth have about the same length and stand in a more or less straight angle towards one another. On the inner border the tip possesses pointed denticles. The marginal tooth with a diameter of 0.03 mm shows a roundish shape with 1 very small hook-shaped cusp.

The animal, found 11 December 1964 with a body length of 5 mm while living, was mature, but the preservation of the anterior genital complex does not permit a precise reconstruction. The situs corresponds in the main features with the situs of *Okenia amoenula* Bergh, 1907 (MACNAE, 1952: fig. 23). There is a well-developed female gland mass, an ampulla, which is tightly filled with sperms and a big, spherical bursa copulatrix. The vas deferens increases to a long prostate tube, which distally decreases into a narrow ductus ejaculatorius, which continues into a tube-shaped penis.

The general body colour is whitish, though some regions of the notum appear yellowish or reddish because of the intestine underneath. The right lobe of the veil, but not the left one, shows at its end a big bright yellow spot. A similar spot covers the tip of the tail. All cerata are yellow from the tip almost to the base, sprinkled with fine clear cadmium-red. The same combination of yellow and clear cadmium-red – which may combine to orange – is to be found on the distal half of the gills and on the median cresta. Dorsally on the right and left side of the notum run 2 irregular stripes of roundish, sometimes very gradually elevated cadmium-red spots towards the tail. Dark cadmium-red spots are also to be observed in the furrow between foot and mantle. The rhinophores are completely opaque-white.

Colour and shape variations: An animal of 4.5 mm body length when alive, found 12 November 1974, pos-

sesses 9 cerata on each side. The last 2 have a common base, on both sides. These last cerata are the longest of all and occupy $\frac{1}{3}$ of the body-length. There is no unpaired appendage medianly behind the gills. The veil has the same shape as in the animal described above, but bears 2 bright yellow lobes. The rhinophores are opaque-white, as well as the tips of the most anterior and most posterior cerata. All other appendages are cadmium-yellow, the notum cresta is yellow with dark cadmium-yellow spots. The tips of the gills, a median stripe on the tail and roundish spots dorsally on both sides of the notum are also dark cadmium-yellow. A 3 mm long specimen found 23 March 1967 has no cadmium-yellow or red at all, but the whole pattern is pale yellow.

DISCUSSION

Shape and colour of the species of the genus *Okenia* are generally so remarkable that many species may be identified by their external appearance. However, as we know nothing about the ecology of most of the species, often only 1 or 2 accidentally dredged specimens are known. To these often questionable species – which have not been found since their original description – belong in the northern Mediterranean: *Okenia dautzenbergi* Vayssière, 1919 (he himself in 1930 placed it in *O. elegans*, but Pruvot-Fol kept it as a separate species) and *O. mediterranea*. PRUVOT-FOL, who believed to have found the latter again (1951: 29), reported (1954: 311), that her unique specimen resembles *O. amoenula* Bergh, 1907 from South Africa. As we have no details from Pruvot-Fol about the radula, genital organs, veil and cerata, we have to confine ourselves to the few statements given in 1951 and 1954: She states that her unique specimen resembles *Okenia elegans* very much, though it possesses only one ceras on the notum. Therefore Pruvot-Fol's specimen probably is neither identical with *O. amoenula* from the Cap (without a median appendage) nor to von Ihering's species (with a smooth notum). Unfortunately von Ihering's species entered into literature with the wrong statements that it possesses 2 tubercles on each side of the median cresta. VON IHERING (1886: 39), however, writes in his description: "Mantel nur am Rande mit Anhängseln." In describing the pattern he writes: "Zwischen Rhinophor und Kiemen, letzteren näher, stehen dann jederseits zwischen Mantelrand und Mittelstreif noch 2 gelbe Flecken, deren Untergrund in Form eines niederen breiten Höckers erhoben ist. Auch der gelbe Mittelstreif ist etwas wulstig erhoben" (1886: 42). In all the external features our specimens correspond completely with von Ihering's statements, also in the shape of the teeth and the peculiar

shape of the labial hooklets, which are denticulated. Besides the smooth notum with a partly elevated cresta, the arrangement and shape of the appendages of the pallial ridge and the large bilobed veil are characteristic for this species. In many external features *Okenia mediterranea* corresponds also with *O. amoenula* Bergh, 1907 (cf. MACNAE, 1958) from South Africa, to which I erroneously assigned the specimens from Naples (SCHMEKEL, 1968). *Okenia amoenula*, however, possesses, according to Bergh's description, smooth labial hooklets and its pattern differs also in details: *O. amoenula* has yellowish, *O. mediterranea*, however, white rhinophores; *O. amoenula* shows 3 crimson stripes on the notum, *O. mediterranea* a broad, median line and next to this roundish spots arranged in 2 lines on each side. The colouration of *O. mediterranea*, however, may vary considerably. Should differences in the labial armature of both species not be confirmed by new investigations, it has to be examined whether *O. amoenula* Bergh, 1907 is a synonym of *O. mediterranea* (von Ihering, 1886), which then has priority.

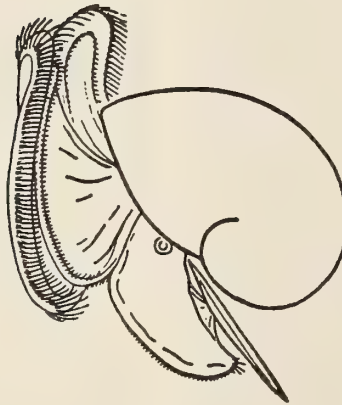
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Malagarion paenelimax gen. nov., spec. nov.,
A New Slug-like Helicarionid from Madagascar

(Pulmonata : Helicarionidae)

BY

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(8 Text figures)

INTRODUCTION

SINCE 1949, Pr E. FISCHER HAS BEEN forming a collection of land snails from Madagascar in the MNHN. This collection now amounts to more than 10 000 lots and is probably the most important in the world for this region; Pr Fischer published more than 30 papers dealing with this material between 1949 and 1977. Most of the material consists of dried shells, but in the small suite of specimens preserved in liquid was found the new Helicarionid here described, which was given by Mrs. F. Blanc who collected it during the 1972 CNRS-RCP 225 expedition in the Marojezy Mountains in the northeast of Madagascar.

Malagarion Tillier, gen. nov.

Diagnosis: A helicarionid with a much reduced shell (less than 2 whorls and almost completely uncalcified) completely covered by the mantle which has no distinct lobes; visceral cavity not entering the posterior part of the foot which is depressed by the visceral hump lying on it. Genital apparatus without a sarcobelum; penis with a penial sheath joining the epiphallus, a flagellum and a short retractor caecum on the outer side of the angle between penis and epiphallus; lower part of the free oviduct inflated and isolated from the upper part by a papilla; vagina and atrium much reduced. Radula with teeth small, very numerous and close-set; the central unicuspid, a few laterals tricuspid and the marginals very numerous (about 300 per half row) and bicuspid.

Type Species: *Malagarion paenelimax* Tillier, spec. nov.

Malagarion paenelimax Tillier, spec. nov.

Material: The holotype.

Type Locality: Marojezy Mountains, 600 m; 12 December 1972; F. Blanc coll. et leg., MNHN.

External Morphology: (Figure 1) Animal 28 mm long in alcohol with a tail 17 mm long and a narrow foot (2.5 mm wide). The visceral hump, completely covered by the mantle without any pore, lies in a triangular depression on the anterior part of the tail (on the holotype this depression is probably accentuated by the position of the animal). The mantle forms a nuchal shield extending forward about halfway to the ocular tentacles. The tail is truncated, without prominent horn, split by the caudal gland which is about as deep as high and triangular in vertical section. The pedal sole is tripartite and limited by a lateral pedal groove. The tegument of the foot is reticulated, with nuchal grooves hardly visible; the reticulation is interrupted above the pedal groove and at a short distance from the truncated posterior end. The mantle is covered with granules which become larger and conical on the back of the visceral hump. The colour in liquid is whitish with the upper part of the mantle and tail finely punctulated with pink, and the nuchal region creamy.

Internal Morphology: The shell has about 1.5 whorls. It is reduced to a horny membrane, except in its last 0.5 whorl where it is slightly calcified with thin concentric growth lines. It is impossible to remove it without breaking either the periostracum or the mantle edge.

The Body Cavity (Figure 2) does not extend at all into the posterior part of the foot. The oesophagus and

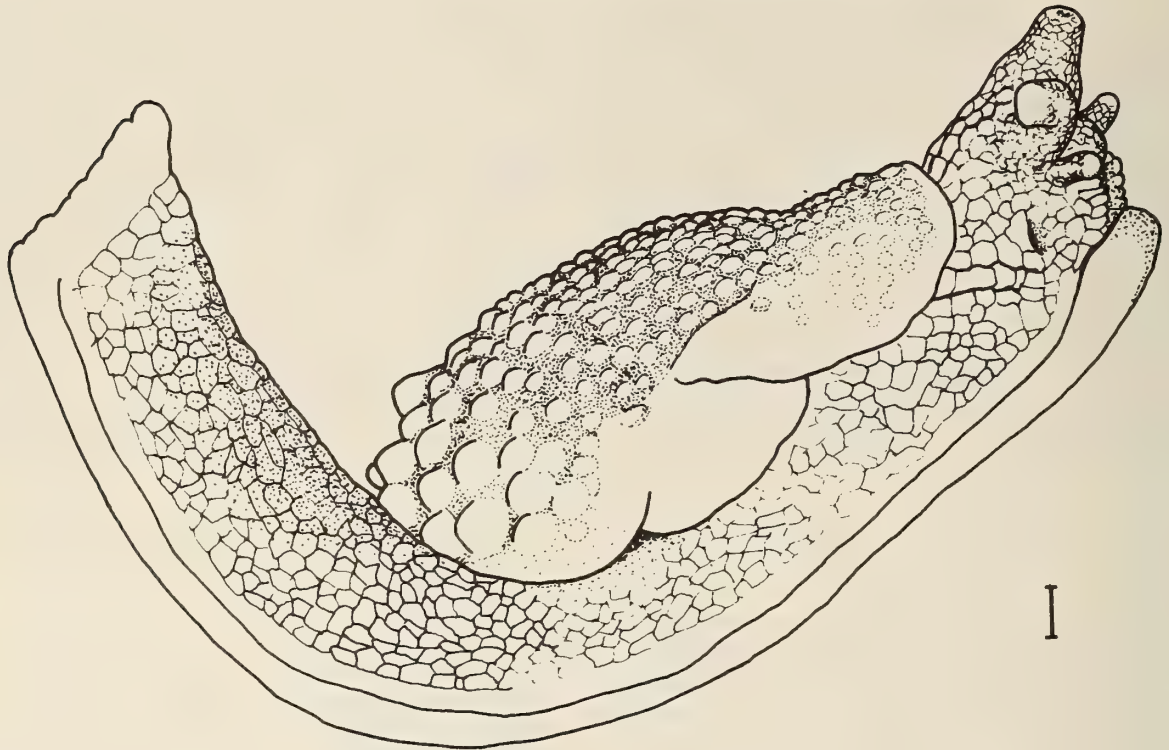


Figure 1

Malagarion paenelimax Tillier, gen. nov., spec. nov.

Habitus of the holotype

(scale: 1 mm)

the enlarged crop lie on the left side, partially embedded in the folds of the oviduct which lies on the right side together with the penis and the bursa copulatrix. The stomach and intestine make 3 loops in the visceral mass, which contains the albumen gland in its concavity and the ovotestis at its extremity.

The free Retractors have 3 insertions along the ligamental back edge of the body cavity; from left to right:

- The left tentacular retractor crosses over the crop and then lies along the left side of the anterior digestive tract;
- The buccal retractors have a large common stem which divides into 2 branches passing through the nerve ring and inserting below the buccal mass;
- The right tentacular retractor runs between the anterior digestive tract and the genital apparatus; it lies on the left side of the latter for its entire length.

The Pallial Complex (Figures 3 and 4) occupies the left anterior half of the visceral hump; kidney, heart and rectum are parallel in a diagonal direction, from the left posteriorly to the right anteriorly. The kidney, very long, is posteriorly reflected into a lobe itself folded in such a way that it is applied to the pericardium on one side and to the second loop of the intestine on the other. The ureter, about of the same diameter as the intestine, overlaps the direct lobe of the kidney before turning back along the rectum; the latter is inflated just anterior to the anus. The external opening is an oblique slit which is divided by a vertical pillar into posterior anus and anterior upper pneumostome and lower kidney pore.

Genital Apparatus: (Figures 5, 6, 7) The small ovotestis is subspherical, blackish and formed by numerous acini. The hermaphrodite duct, rather short, becomes

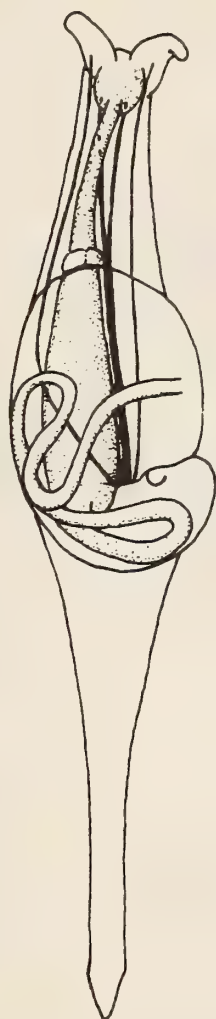


Figure 2

Malagarion paenelimax Tillier, gen. nov., spec. nov.

Disposition of the digestive tract and of the free retractors
(rhinophoral branches of the tentacular retractors not depicted)

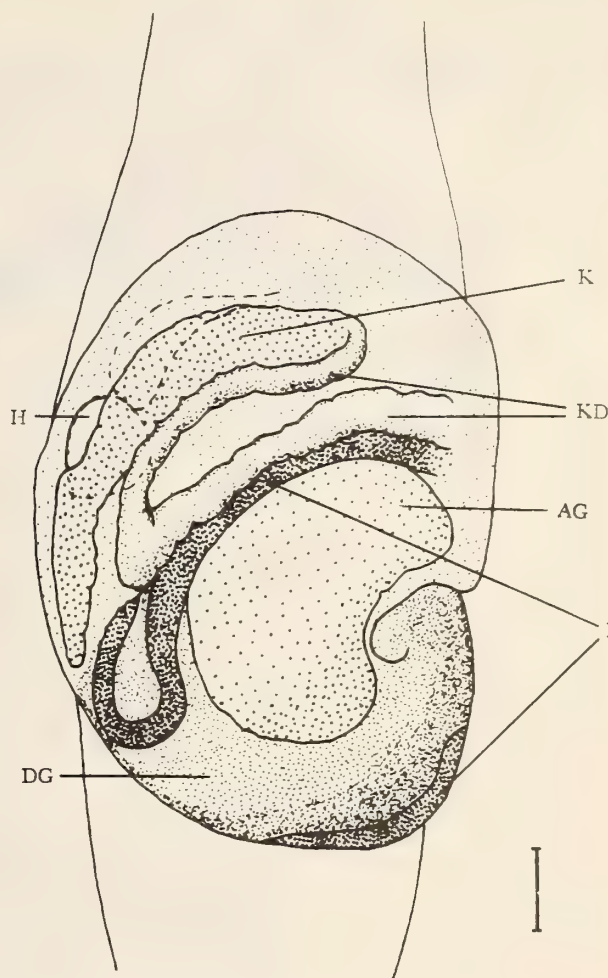


Figure 3

Malagarion paenelimax Tillier, gen. nov., spec. nov.

Disposition of the organs in the visceral hump, upper view
AG - albumen gland DG - digestive gland H - heart
I - Intestine K - kidney KD - Kidney duct
(scale: 1 mm)

broader and twisted in its distal part. It opens into the spermooviduct at the base of a short and broad talon applied on the concave side of the albumen gland. The spermooviduct is subcircular in section in its first half, but in its second half the oviduct forms large flat expansions in which the anterior digestive tract is partially embedded *in situ*. The free oviduct is divided into 3 sections: the first

has a thick orange wall and is probably glandular; the second is a simple tube which opens by a prominent constricted papilla into the third. The latter, which may be involved either in the secretion of the shells of the eggs or, by analogy with *Colparion*, in their incubation, is a greyish, thick walled and curved pouch and has a large and internally folded opening at the base of the bursa

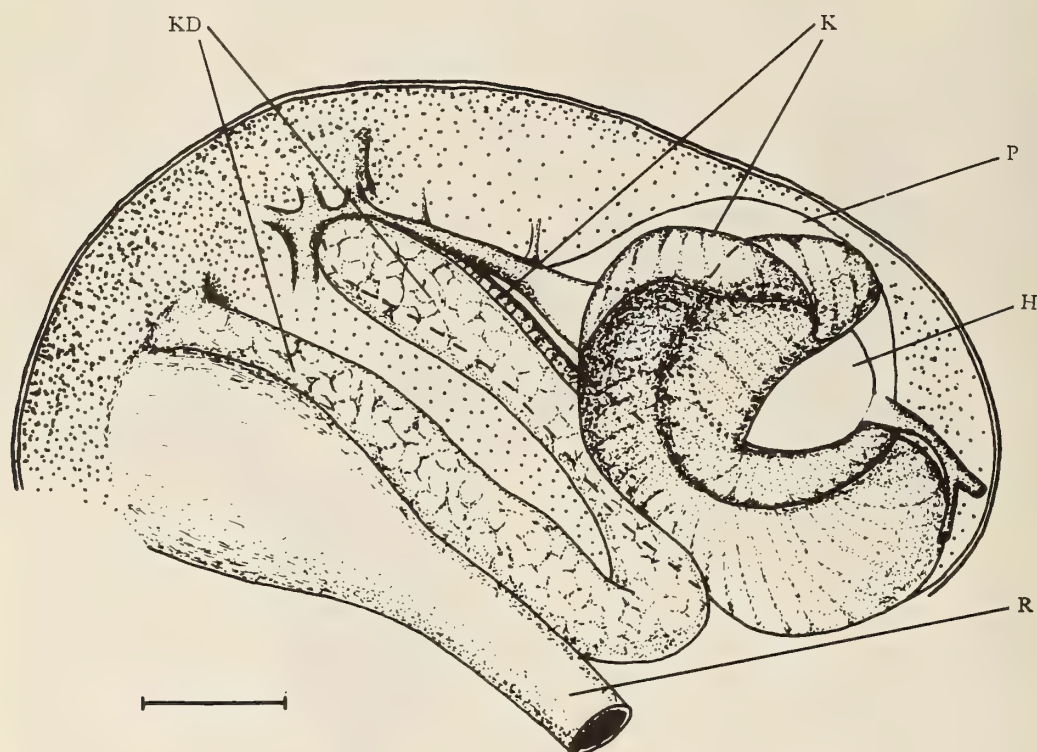


Figure 4

Malagarion paenelimax Tillier, gen. nov., spec. nov.

Pallial complex, lower view

H - heart

K - kidney

KD - kidney duct

P - pericardium

R - rectum

(scale: 1 mm)

copulatrix. Except for these few folds and the papilla, the inner wall of the oviduct is smooth.

The bursa copulatrix is rather short and finger-like. Its inner wall is smooth in its inferior third, and has transverse regular folds in its upper two thirds. The oviduct and the bursa copulatrix open without a distinct vagina into the genital atrium, which is reduced as much as possible and internally smooth.

The penial complex (Figures 6 and 7) has a sheath, a short retractor caecum inserted on the outer side of the angle between penis and epiphallus, and a flagellum. The epiphallus and flagellum are bent back along the penis, the former being connected to the penial sheath by a tract.

The penis is divided into 2 subequal parts by a penial papilla. Just above and below this papilla the penis is inflated and internally granulous whereas it is tubular with internal longitudinal folds in its lower and upper parts. Just below the penial papilla a second papilla is inserted; it is folded and triangular when flattened. The penis has 2 sheaths: the lower one, thicker and with circular fibres in its lower part, encloses the lower tubular part of the penis and is joined to the epiphallus by a thin connective tract; the upper penial sheath is much thicker and encloses only the upper bulbous part of the penis. The caecum prolongs the penis and is bent along the epiphallus; it is short, not coiled, thin walled and has internal longi-

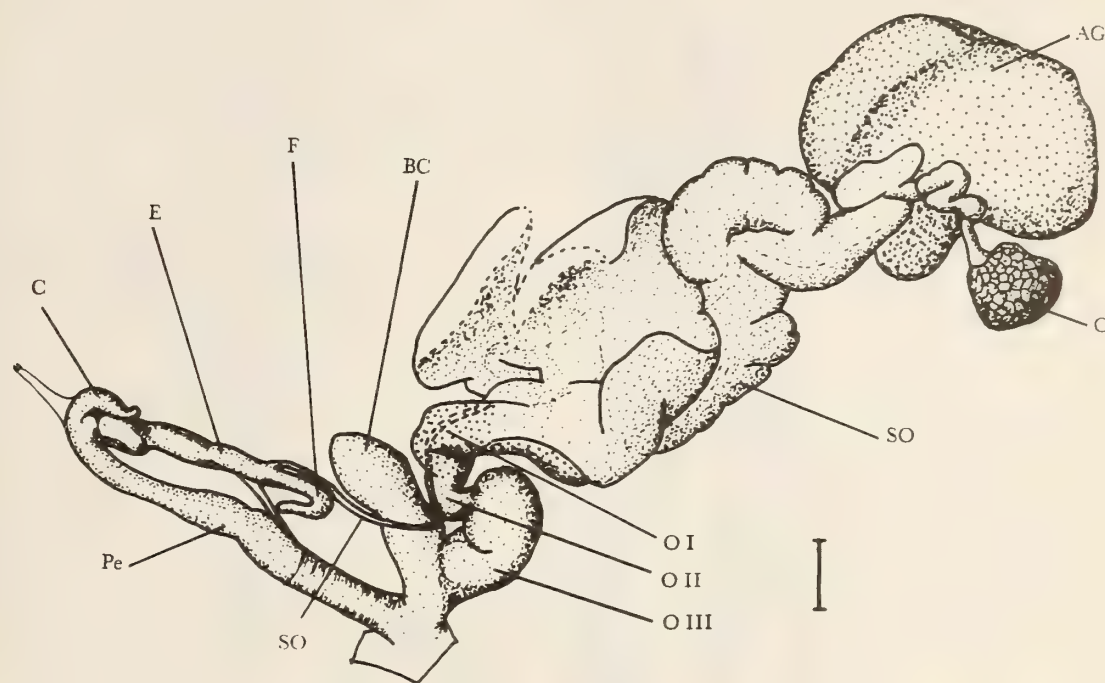


Figure 5

Malagarion paenelimax Tillier, gen. nov., spec. nov.

Genital apparatus:	AG - albumen gland	BC - bursa copulatrix
C - caecum	E - epiphallus	F - flagellum
HD - hermaphrodite duct	OI, OII, OIII - sections of the free oviduct	
Pe - penis	SO - spermoviduct (scale: 1 mm)	

tudinal folds, except in its basal region where the folds are honeycomb-like. The epiphallus opens into the penis at the base of the caecum by a narrow and prominent papilla. Its inner wall is also longitudinally folded except around the opening of the vas deferens where it is smooth. It is bent in its thin sheath which adheres to its wall at the convexity of the bends. The flagellum is a hollow tube, internally smooth, with its axial cavity occluded by a rod which is cylindrical near its fixed extremity and then flattened with its free end enlarged; such a structure was previously described by VAN MOL (1968, 1970). The extremity of the flagellum is bent back, with a thin sheath visible in the convexity of the bend.

No horny spermatophore was found, but the bursa copulatrix was filled with whitish, soft fragments; on the other hand, the epiphallus contained a mass of the same

material which disintegrated when dissected. This suggests, but does not prove, the occurrence of a soft spermatophore; if a horny spermatophore is found later on, it will probably be smooth as a result of the absence of crypts in the inner wall of the flagellum.

The Radula (Figure 8) is formed by 132 V-shaped rows, with an angle of about 130° , and more than 600 teeth per row; formula:

$$(300 \pm 15) \cdot (3 - 6) \cdot C \cdot (3 - 6) \cdot (300 \pm 15).$$

All the teeth have very long basal plates, nearly extending to the extremity of the cusps and parallel to the upper plates. The central is unicuspid, elongated, about $30 \mu\text{m}$ long. The lateromarginals are elongated too, very tight and slightly sigmoid, becoming progressively smaller when approaching the end of the rows. The first ones are tri-

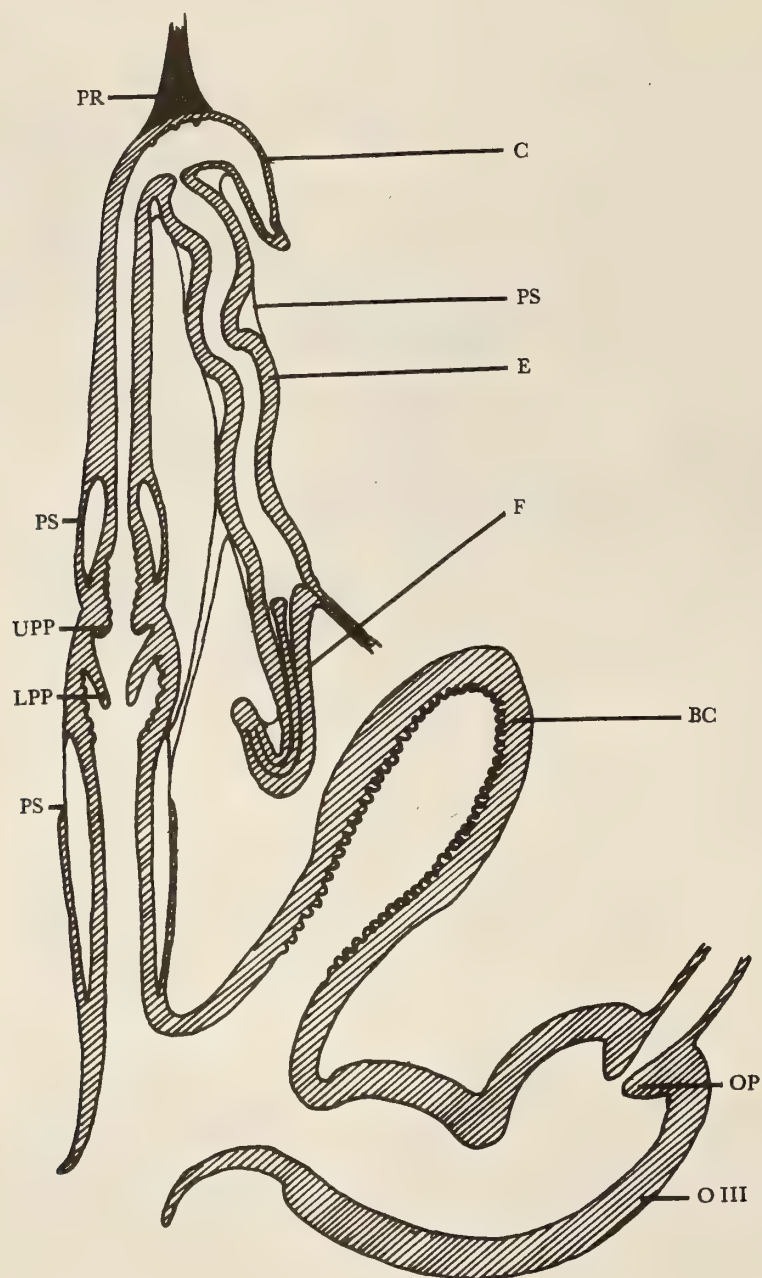


Figure 6

Malagarion paenelimax Tillier, gen. nov., spec. nov.

Longitudinal section of the lower genitalia: BC - bursa
 copulatrix C - caecum E - epiphallus F - flagellum
 OIII - lower section of the free oviduct PR - penial retractor
 PS - penial sheath OP - papilla of the oviduct UPP -
 upper penial papilla LPP - lower penial papilla

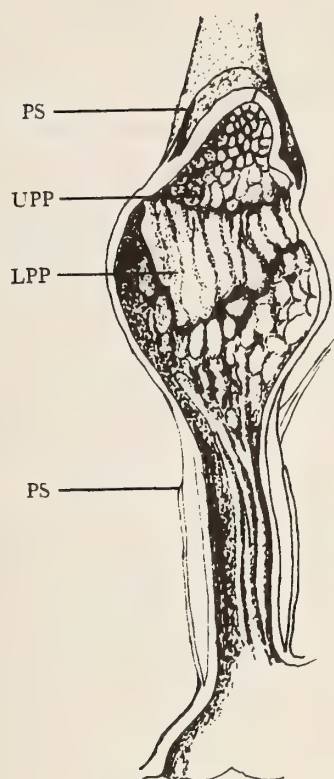


Figure 7

Malagarion paenelimax Tillier, gen. nov., spec. nov.

Lower penis opened and flattened:

PS - penial sheath

UPP - upper penial papilla

LPP - lower penial papilla

cuspid with a large mesocone; then the endocone disappears and at the same time the ectocone becomes larger than the mesocone. This feature is preserved as far as the last and smallest marginals.

The conical papillae of the mantle showed a spongy structure when cut under the binocular microscope. Histological preparations exhibited numerous lacunae within them; these lacunae open outwards by numerous pores on each papilla. Unfortunately the animal was too badly fixed to allow further histological investigations, but it seems that these lacunae are reservoirs for a liquid which may be exuded: it could be a repellant material, not uncommon in zonitoid snails; but this is only a hypothesis.

Ecology: The Marojezy is one of the best preserved Malagasy mountains; its isolation prevented its slopes from being burnt like those of other mountains. It has the greatest rainfalls in Madagascar. At the altitude of 600 m, where *Malagarion paenelimax* was found, its slopes are covered by evergreen rain forest. Complete data concerning rainfalls, temperature and insolation of the collecting station may be found, with additional references about the Marojezy and its vegetation, in GUILLAUMET *et al.* (1972).

DISCUSSION

The only species related to *Malagarion paenelimax* seems to be *Colparion madgei* Laidlaw, 1938, only species of the genus, described from Rodrigues Island. They have mainly in common a reduced shell and the lack of a sarcobellum, but they show some other similar trends: they have

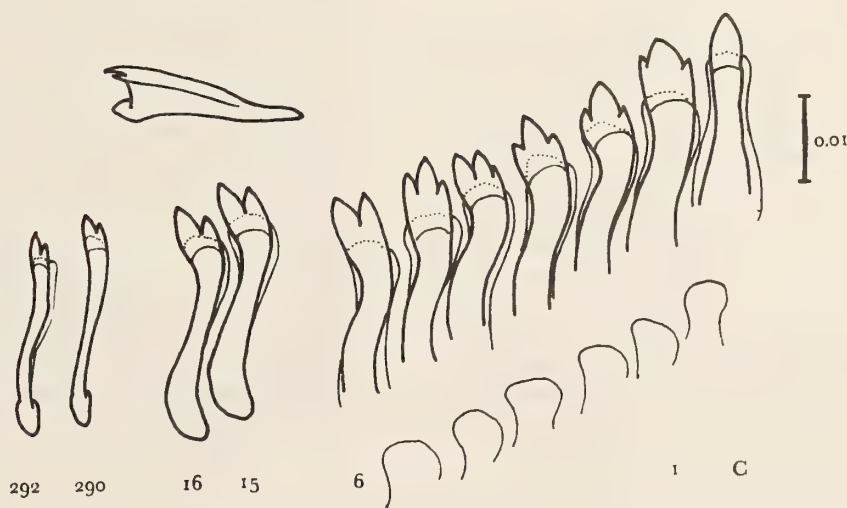


Figure 8

Malagarion paenelimax Tillier, gen. nov., spec. nov.

Radula: on the upper left, side view of a marginal tooth (about the 200th)

the number of teeth per row larger than is common in the helicarionids and larger than in any known Malagasy species (250 in *Colparion* and 600 in *Malagarion*); both have a similar penial organization, with a long flagellum, a short retractor caecum inserted in the same way and with a penial sheath (although not mentioned by Laidlaw, a penial sheath seems to occur in his figs. 1-2). Their external appearance seems also to be similar, with nuchal grooves only slightly marked and the tail depressed under the visceral mass which does not extend backward into the foot. However, their differences, in particular in the degree of overlapping of the shell by the mantle and in the radula, do not allow assigning them to a single genus.

The genus *Colparion* was placed by BAKER (1941), whose classification as modified by SOLEM (1966) is followed here, among the Helicarioninae on the basis of the lack of a sarcobelum; but now we know that this is not a suitable character for the determination of the systematic position, and that a sarcobelum can appear independently in parallel lineages (VAN MOL, 1970); so the position of *Colparion* and *Malagarion* has to be discussed here.

These two genera cannot be placed among the Urocyclinae (= Trochozonitinae + Urocyclinae auct.: the works of van Mol and van Goethem clearly show that the classical distinction cannot be maintained); independently of the structure of the sarcobelum, the Urocyclinae show after van Mol (*in lit.*) slight but constant differences from the other helicarionids: in particular their penial sheath always joins the penis above the penial papilla and, when the shell is reduced, the visceral cavity extends into the caudal region (except in *Tresia* and *Leptichnus*, cf. VAN GOETHEM, 1977).

Neither of our two genera shows any of these features, but on the contrary they show striking similarities with various Ariophantinae: gross organization of the penial complex (cf. *Macrochlamys* VAN MOL, 1968); organization of the penial sheath (cf. *Sesara* and the Girasii, SOLEM, 1966; Madagascan *Kalidos*, van Mol, *in lit.*); presence of two papillae in the penis (*Oxytes*, BAKER, 1941; *Megaustenia*, SOLEM, 1966); large number of radular teeth per row (cf. the Durgelli). At first glance the radula and the reduction of the shell suggest affinities with the Durgelli; however, the latter show a constant penial organization, without any flagellum and with the penial retractor close to the vas deferens, which is quite different from that of *Colparion* and *Malagarion*. In spite of some similarities it seems also difficult to place

our two genera among the Girasii, which have an epiphallic retractor caecum, a different reflexion of the penial complex from the penial retractor and usually a blunt flagellum. Whatever tribe, as defined by SOLEM (1966), is considered, *Malagarion* shows features too aberrant to be classified in one of them as far as known intermediate forms are lacking. At the moment it seems best to consider *Colparion* and *Malagarion* as representative of a Malagasy lineage parallel to the other tribes of the Ariophantinae and possibly originating in the Macrochlamydi, which have both plesiomorphic characters and a diversity in the organization of the penial complex greater than in other tribes; but this view is only tentative and needs to be confirmed by further anatomical investigations of the Malagasy Ariophantinae.

ACKNOWLEDGMENTS

The author is grateful to Pr Fischer-Piette who has entrusted him with this interesting snail and to Dr. J.-J. van Mol for discussions on its taxonomic position.

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A Fossil *Haliotis* from the Galápagos Islands

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(2 Plates)

AMONG THE IMPORTANT results of the 1964 Galápagos International Scientific Project was the discovery of fossiliferous deposits intercalated among an older volcanic sequence (DURHAM, 1965). These older rocks underlie the younger volcanic rocks that are exposed over most of the surface of the islands. These older fossiliferous rocks have a late Miocene age (DURHAM & MCBIRNEY, 1975) and crop out in several places along the east coast of Santa Cruz Island, northeast of Academy Bay. Marine fossils occur in them at several different localities. The fossil collections made at these places are in the Museum of Paleontology of the University of California at Berkeley (hereinafter abbreviated as UCMP).

These Galápagos fossil collections are quite diverse in their contents but have not been studied in detail. They contain numerous Mollusca, Bryozoa, ahermatypic corals, barnacles, echinoid spines and calcareous algae. Among the more conspicuous fossils is a large pecten that is difficult to differentiate from *Lyropecten crassicardo* (Conrad, 1857) of the California upper Miocene. At one locality (UCMP B-3612) a very diverse fauna was found. The ahermatypic corals present suggest that the deposit was formed at depths of 10 m or somewhat more. The field observations plus some of the rock-inhabiting taxa present suggest that it was formed at the base of a steep shore, perhaps even a cliff of basalt. One of the obvious fossils collected was a small *Haliotis*. Because fossil haliotids are rare and because this specimen is not assignable to the living Galápagos species, *Haliotis dalli* Henderson, 1915, it is described in this note.

James H. McLean and Gale Sphon of the Los Angeles County Museum (hereafter abbreviated LACM) have generously loaned me specimens of *Haliotis dalli* and *H. roberti* for comparison and permitted me to illustrate them. The manuscript has benefited from discussions with Carole S. Hickman and Joseph H. Peck, Jr.

SYSTEMATICS

Haliotis Linnaeus, 1758Type species: *Haliotis asinina* Linnaeus, 1758

The shell of *Haliotis asinina* is very elongate and narrow, with a very eccentric apex. Few species are assignable to the typical subgenus. In the Treatise on Invertebrate Paleontology (MOORE, 1960), 11 subgenera of *Haliotis* are recognized. FLEMING (1952) has also discussed some of the haliotid supraspecific taxa. *Haliotis dalli* Henderson, 1915 from the Galápagos Islands and *H. roberti* McLean, 1970 from Cocos Island have both been referred to the subgenus *Padollus* Montfort and the new fossil species seems to belong to the same group.

(Padollus) Montfort, 1810Type species: *Padollus rubicundus* Montfort, 1810, ?=
Haliotis scalaris Leach, 1814

This subgenus is characterized by fairly tight coiling, a spire rising above the general whorl surface, a broad spiral rib, with corresponding groove on the interior, ad-apical to the row of tremata, spiral cording, and whorl periphery extending beyond labral margin (see Figure 10).

Neither *Haliotis roberti* nor the common variants of *H. dalli* have been well illustrated. Inasmuch as excellent material of each species is available as well as some unpublished distributional data, both species are here illustrated, discussed, and compared with the fossil species.

Haliotis (Padollus) dalli Henderson, 1915

(Figures 1, 2, 3, 4, 5)

Haliotis pourtalesii ? DALL, 1890 (not 1889): 355; pl. 12
figs. 1, 3; - STEARNS, 1893: 418, 448

- Haliotis pourtalesii* PILSBRY, 1890, Man. Conch. (1) 12: 121; plt. 22, figs. 27, 28, non DALL, 1881
Haliotis (Padollus) dalli HENDERSON, 1915: 661; pls. 45, 46, lower figs.; - KEEN, 1971: 308, 311 (fig. 1); - ABBOTT, 1974: 18, no. 32

Seventeen specimens of this uncommon species have been available for study. They show much variation in height of spire, heaviness of cords, and presence or absence of undulating radial ribs. The most constant feature is the number of spiral cords at a given diameter. New cords are added by intercalation with increase in size; as a result the relative strength of a cord may increase from its inception to the aperture. On the largest specimen (Figure 2) there are about $1\frac{1}{2}$ nuclear whorls before the first trema appears; at this point there are about 10 cords above the trema - at the apertural edge there are about 52. On this specimen there are 27 tremata (plus one partial), of which at least 4 are open. The heaviness of the cords is variable (compare Figures 1 and 3) as is the presence of radial ribs. The type specimen as figured by HENDERSON (1915) lacks radial ribs and the spiral cords are only moderately developed. The specimen illustrated in Figure 1 approaches the type rather closely except that it is somewhat smaller. The specimen illustrated in KEEN (1971: 311; fig. 1) and refigured here (Figure 3) has

Explanation of Figures 1 to 8

Specimens in Figures 1 to 5 photographed with apertures resting on horizontal surface

- Figure 1: *Haliotis (Padollus) dalli* Henderson, LACM loc. 148-34, ornamentation compares well with that of holotype as figured by HENDERSON (1915) $\times 4$
 Figure 2: *Haliotis (Padollus) dalli* Henderson, LACM loc. 72-197, variant with low spire and strong radial ribs $\times 3$
 Figure 3: *Haliotis (Padollus) dalli* Henderson, LACM loc. 30142, variant with high spire and moderate radial ribs (specimen illustrated by KEEN, 1971: 311, fig. 1) $\times 3$
 Figure 4: *Haliotis (Padollus) dalli* Henderson, LACM loc. 72-197 variant with low spire and moderate radial ribs $\times 2.7$
 Figure 5: *Haliotis (Padollus) dalli* Henderson, same specimen as Figure 4, lateral view $\times 6$
 Figure 6: *Haliotis (Padollus?) santacruzensis* Durham, spec. nov. UCMP 14589, loc. B-3612 $\times 6.7$
 Figure 7: *Haliotis (Padollus?) santacruzensis* Durham, spec. nov. same specimen as Figure 6, lateral view $\times 5.5$
 Figure 8: *Haliotis (Padollus) roberti* McLean, holotype, LACM 1368, lateral view $\times 6$

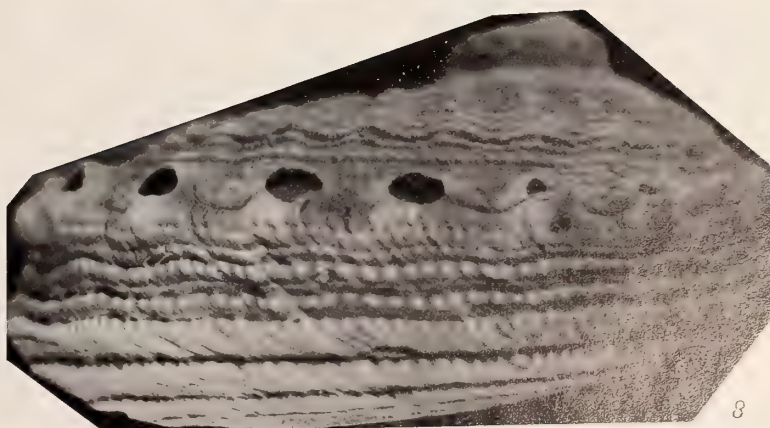
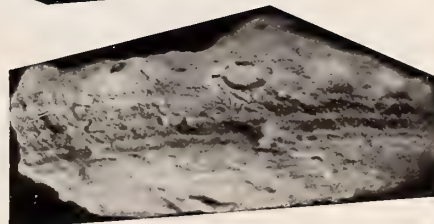
heavily developed cords and well marked radial ribs in contrast to a similar sized specimen (Figure 2) with strongly developed radial ribs and less strongly developed cords. Similar sized specimens vary considerably in proportions (measurements made with aperture on a horizontal surface). The 2 largest specimens (Figures 2, 3) have major diameters of 27.1 and 27.4 mm; their respective heights (not height of spire) are 10.7 and 8.4 mm, the number of tremata $28+$ and $27+$. The total height (axis of coiling vertical) is about 16 and 20 mm.

The tremata are formed by periodic constrictions (Figures 5, 8) of a slit (which begins at the end of the nuclear whorls) in the outer layers of the shell. The older tremata are closed by deposition of the innermost nacreous layers. The constrictions are formed by projections

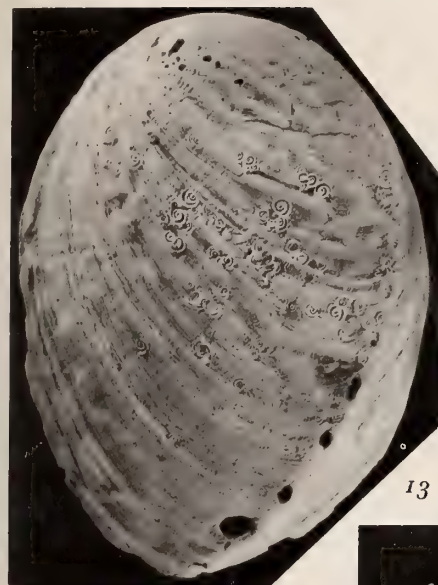
Explanation of Figures 9 to 17

Specimens in Figures 9, 11, 12, 13, 15 photographed with apertures resting on horizontal surface

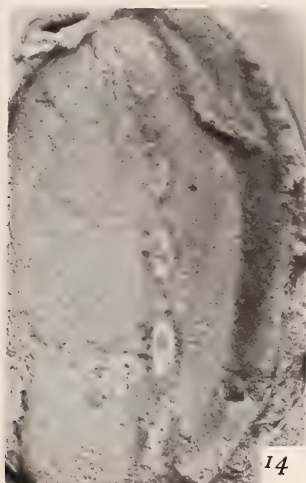
- Figure 9: *Haliotis (Padollus) roberti* McLean, paratype, LACM 1369, apertural edge broken $\times 4$
 Figure 10: *Haliotis (Padollus) dalli* Henderson, LACM loc. 30142 (same specimen as Figure 3), apertural view of high spired individual showing smooth flattened columellar lip (lower right and subcentral) $\times 2.9$
 Figure 11: *Haliotis (Padollus) dalli* Henderson, LACM loc. 30143, high spired individual with moderate radial ribs (attached homotrematid foraminifera below spire) $\times 3$
 Figure 12: *Haliotis (Padollus) roberti* McLean, holotype, LACM 1368, same specimen as Figure 8 $\times 3$
 Figure 13: *Haliotis (Paua) iris* Martyn, hypotype UCMP 14590, loc. D-7558, apical whorls very eccentric $\times 0.88$
 Figure 14: *Haliotis (Paua) lomaensis* Anderson, holotype CAS 69, oblique view of latex cast (apex at top) of interior of incomplete external half of holotype (shell material preserved) showing 4 open and 2 closed tremata at top $\times 6$
 Figure 15: *Haliotis (Paua) lomaensis* Anderson, holotype, CAS 69, nearly entire specimen except for missing shell material (attached to original of Figure 14). Apical whorls at center of top, note outer lip extending around apex and joining columellar flange on right side $\times 6$
 Figure 16: *Haliotis (Paua) iris* Martyn, same specimen as in Figure 13, aperture inclined, note outer lip extending around apical whorls and merging with columellar flange $\times 0.88$
 Figure 17: *Haliotis (Paua) iris* Martyn, interior of same specimen as in Figures 13 and 16, note impressed adductor muscle scar and pallial line (lower left) as well as smooth inner surface of combined outer lip-columellar flange on right side $\times 1$







13



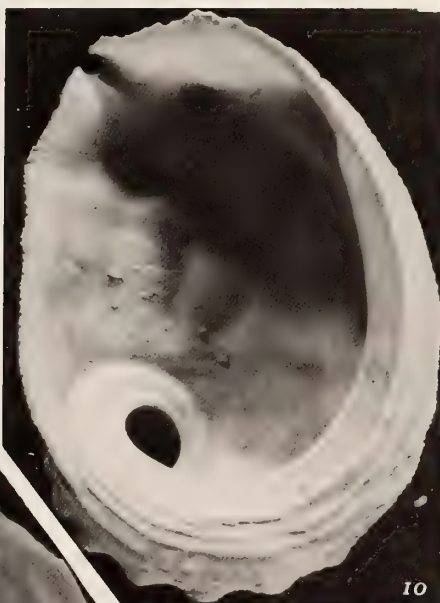
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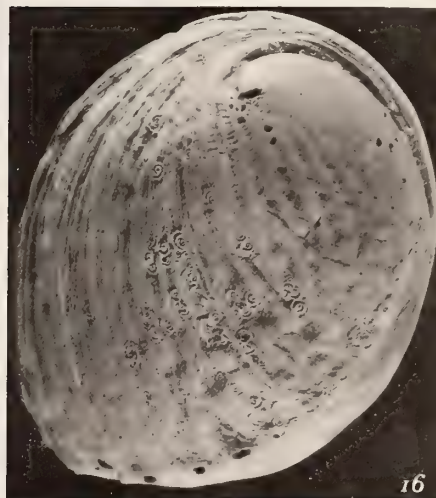
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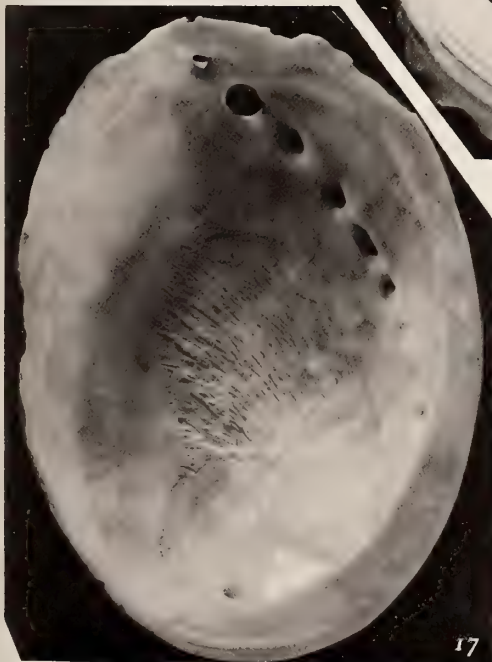
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11



12

of the outer shell layers, with the projection from the adapical side overlapping that from the adoral side. Examination of several other species of *Haliotis* shows a similar mode of formation of their tremata.

Occurrence: Fifteen specimens examined are from the Galápagos Islands, from intertidal to depths of about 110 m. They are from LACM localities 30142, 30143, 30144, 66-210, 72-197, AHF 147-34, AHF 148-34, and AHF 198-34. Most specimens are from depths around 60 m, but the largest (Figure 2) is from the intertidal zone. Two specimens (LACM loc. AHF 81-38) are from north of Gorgona Island, Colombia, depth between 18 and 36 m.

Haliotis (Padollus) roberti McLean, 1970

(Figures 8, 9, 12)

Haliotis (Padollus) roberti McLEAN, 1970: figs. 1-2; - KEEN, 1971: 309, 311 (fig. 2); - ABBOTT, 1974: 18, 19; fig. 33

Nine specimens, including the holotype and 2 paratypes of this species from Cocos Island have been available, but 3 of them are very small and worn. The spiral ridge characteristic of *Padollus* is well developed only on specimens from locality LACM 73-176. At similar sizes there are fewer and heavier spiral cords above the tremata and on the periphery below them than on *Haliotis dalli*. Further, the body whorl is more inflated than on the Galápagos species. However, there are more spiral cords than on the new fossil species. The measurements (made in the same manner as for *H. dalli*) of the holotype (Figures 8, 12) are: major diameter 18.6 mm; height 6.6 mm; total height (axis of coiling vertical) about 12.5 mm.

Occurrence: Known from Chatham Bay, Cocos Island, Costa Rica, between 73 and 86 m in depth and nearby Isla Manuelita at depths of 146 and 174 m (LACM locs. 73-116 and 73-117).

Haliotis (Padollus?) santacruzensis Durham, spec. nov.

(Figures 6, 7)

Described on the basis of a single incomplete specimen (original major diameter about 12 mm) with aperture filled with matrix. Shell profile similar to that of *Haliotis dalli* and not inflated like *H. roberti*; a distinct concave area below trematal angulation; spiral cording suggestive of *H. pourtalesii* Dall, 1881 as illustrated by ABBOTT (1974: 18, fig. 30), but cords less numerous at similar

sizes; at a diameter just under 10 mm (see Figure 6) there are 9 or 10 major cords above the tremata and 4 in the concave area (see Figure 7) below the tremata; the sub-trematal area is very similar to that of Abbott's figure; the spacing of the tremata seems to be about the same as on a similar sized specimen of *H. roberti* (Figure 9); although not well preserved, there appear to be 3 or 4 spiral cords on the oral surface below the lowermost peripheral whorl angulation (see Figure 7), much like those on *H. dalli* (see Figure 5).

Holotype: UCMP 14589, loc. B-3612, near Cerro Colorado, northeast of Academy Bay, Santa Cruz Island, Galápagos Islands.

Age: Late Miocene (DURHAM & MCBIRNEY, 1975: 286 to 287)

Discussion: This species differs from *Haliotis barbadensis* Trechmann, 1937, *H. dalli* Henderson, *H. roberti* McLean, and *H. pourtalesii* Dall by the fewer cords above the tremata at similar sizes; the upper whorl profile is not as inflated as in *H. roberti* or *H. pourtalesii* (judging from ABBOTT, 1974: 18, fig. 30). The elevated ridge and corresponding internal groove above the row of tremata that is characteristic of most specimens of this group of species is not clearly evident on this specimen, but in view of its general similarity to *H. dalli*, *H. pourtalesii*, and *H. roberti* it is tentatively referred to *Padollus*, the subgenus to which these species have mostly been referred. The 4 (*H. pourtalesii*, *H. dalli*, *H. barbadensis* and *H. roberti*) appear to be closely related and it is probable that *H. santacruzensis* spec. nov. represents the parental stock that was living in the tropical eastern Pacific-Caribbean region before the Late Tertiary division of the area by the formation of the Central American landmass and the filling of the northwest Colombian trough.

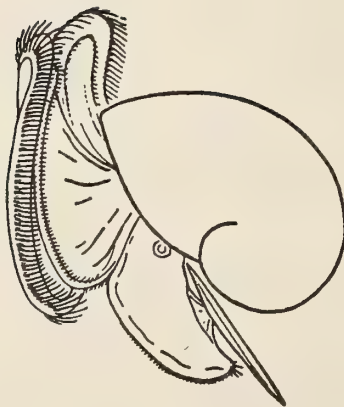
JUNG (1968), without discussion, referred both *Haliotis pourtalesii* and *H. barbadensis* to the subgenus *Sulculus*, rather than to *Padollus*, as previous authors had done. The type of *Sulculus* is *H. incisa* Reeve, 1846, which as illustrated in *Conchologica Iconica* has the apex nearly marginal and a rapidly expanding body whorl, unlike the species discussed above. It is improbable that they should be assigned to *Sulculus*. *Haliotis pourtalesii* was referred to *Padollus* by DALL (1881; 1890) and HENDERSON (1915). Although the critical ridge is not apparent in the inadequate illustrations of FOSTER (1946), GUICE (1968) and ABBOTT (1974), those of HARRY (1966) and JUNG (1968: figs. 7-9) confirm its presence. The Caribbean and Eastern Pacific species discussed herein have less eccentric apical whorls than in *Sulculus* and a closely coiled body whorl, like those of the type of *Padollus*. The raised

ridge (and corresponding internal groove) adapical to the tremata is not as strongly developed as in typical *Padollus*, but in view of its presence, these species are best assigned to this subgenus. Trechmann's species was referred to the late Pliocene by Jung, but the "Coral-rock" in which it is found is currently referred to the Pleistocene. If the Galápagos species is correctly referred to *Padollus*, it extends the range of *Padollus* back to the Miocene.

This is the second (Trechmann's species was the first) fossil *Haliotis* to be described from the tropical region of the Americas and adjacent islands, although Cretaceous (ANDERSON, 1902), Miocene (WOODRING, 1931; 1932; HERTLEIN, 1937) and Pliocene (VOKES, 1935) species have been described from California.

Literature Cited

[see combined list at end of following paper (DURHAM, California's Cretaceous *Haliotis*)]



California Cretaceous *Haliotis*

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(with part of 1 Plate)

AT THE BEGINNING of this century, F. M. ANDERSON (1902: 75; pl. 9, fig. 183) described a small fossil *Haliotis* from the Upper Cretaceous of Point Loma, near San Diego, California. The specimen, associated with *Pecten californicus* and *Acteonina pupoides*, had been collected by H. W. Fairbanks from "...below the beds contain[ing?] *Coralliochama orcutti* according to the statements of Dr. Fairbanks." It was illustrated by a crude pencil drawing (repeated in ANDERSON, 1958: pl. 21, fig. 12). Although ANDERSON in his original description (1902: 75) noted its resemblance to *Haliotis iris*, the systematic position of the specimen has been doubted. WOODRING (1931: 35) was sceptical of its generic assignment and COX (in MOORE, 1960: 221-222) noted that it and other putative Cretaceous haliotids needed to be confirmed. VOKES (1935: 251), after examination of the holotype, affirmed that it was a true *Haliotis*, as did HERTLEIN (1937). I have examined the specimen and because it has never been adequately illustrated and clearly is similar to *H. iris* as stated by Anderson, I am illustrating it photographically.

The specimen is now in the type collection (no. 69) of the Department of Geology of the California Academy of Sciences (CAS), San Francisco. It is in 2 parts, imbedded in a fossiliferous hard, dark gray-green gritty fine sandstone. The associated fossils include fragments of a small oyster, calcareous algae, an echinoid spine, a cross section of a gastropod, a serpulid tube, an external mold of a small fragment of a heteromorph ammonite, and a fragment of a pelecypod. Anderson reported that it came from below the *Coralliochama* horizon at Point Loma. The lithology of the matrix suggests that the specimen came from the Kr(b) member (above basal redbeds) of the Rosario Formation as shown in the columnar section of MILOW & ENNIS (1961: 26 and 36, Stop #10). POPENOE, IMLAY & MURPHY (1960) assigned the Rosario Formation at Point Loma to the Lower Maestrichtian, although they implied that there is some uncertainty as to whether the formation extends down into the Campanian. Thus, it is probable that Anderson's species is of early Maestrichtian age but it might possibly be of latest

Campanian age. It is clear that *Haliotis* was present in the late Cretaceous of California.

The type specimen is very similar to small specimens of *Haliotis iris* Martyn, 1784, the type species of the subgenus *Paua* Fleming, 1952, so *H. lomaensis* is assigned to this subgenus.

This paper has benefitted from discussions with Carole S. Hickman and Joseph H. Peck, Jr.

SYSTEMATICS

Haliotis Linnaeus, 1758Type species: *Haliotis asinina* Linnaeus, 1758

The shell of *Haliotis asinina* is very elongate and narrow, with the apex very eccentric. Very few species are similar to it and assignable to the typical subgenus. In the Treatise on Invertebrate Paleontology (MOORE, 1960) 11 subgenera are recognized. FLEMING (1952) reviewed some of these when he proposed the subgenus *Paua*.

(Paua) Fleming, 1952Type species: *Haliotis iris* Martyn, 1784 (figured herein, Figures 13, 16, 17)

Shell of few whorls, last whorl rising above apex; outer lip extending around behind apex for about a half volution (see Figure 16) and overlapping the columellar flange (in Fleming's diagnosis, the terminology is confusing), which forms a broad posterior labral area; a slight angulation at the row of tremata; mature shells with adductor scar deeply incised but not apparent on small shells; posterior labral area forms posterior shell margin; ornamentation collabral and sometimes with faint oblique undulations and inconspicuous spiral cords.

According to the Treatise on Invertebrate Paleontology (MOORE, 1960: 1223) *Paua* has a range of Miocene to Recent in New Zealand and Japan; the assignment of *Haliotis lomaensis* to the subgenus extends it back to the late Cretaceous. This suggests that *Paua* may be near

the ancestral stock of the haliotids, but it is highly specialized in the greatly enlarged body whorl. The types of the 2 other reputed Cretaceous haliotids, *H. antiqua* Binkhorst, 1861, and *H. cretacea* Lundgren, 1894, need to be restudied.

Haliotis (Paua) lomaensis Anderson, 1902

(Figures 14, 15)

Haliotis lomaensis ANDERSON, 1902: 75; pl. 9, fig. 183; - WOODRING, 1931: 34-35; - VOKES, 1935: 251 - ANDERSON, 1958: 146; pl. 21, fig. 12 (reprint of 1902 drawing)

Shell small, length 13 mm, width 9.6 mm; outermost surface poorly preserved, but most of shell present; apex very eccentric, with at least one volution (very similar to *Haliotis iris*, compare Figures 13 and 15); last 4 tremata open and at least 2 earlier ones closed; shell profile with slight angulation along row of tremata; outer lip extends well around spire (see Figure 15) overlapping columellar flange as in *H. iris*; posterior labral area forms shell margin; microstructure of shell where observable suggests that there may have been inconspicuous spiral cords.

The shell is somewhat recrystallized and the nacreous character of the inner layers lost although in some areas the laminated character of the original nacre is still apparent. Anderson's original drawing suggests the presence of a ridge just adapical to the row of tremata - this part of his drawing is based on the internal mold of this area of the shell and actually represents a low ridge on the interior (not exterior) of the shell just adapical to the tremata. None of the specimens of the Recent *Haliotis iris* that have been examined have this structure. No evidence of a strongly impressed adductor muscle scar can be recognized on Anderson's type, but the internal surface of the shell is not well preserved in the area where it would be expected.

The very eccentric small apex, outer lip extending around posterior to apex and merging with columellar flange, and the combined flattened columellar flange - outer lip forming the posterior margin of the shell indicate that this species should be assigned to the subgenus *Paua*.

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Chlamydoconcha orcutti Dall: Review and Distribution of a Little-Known Bivalve

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THE INTERNALLY-SHELLED epifaunal veneroid clam *Chlamydoconcha orcutti* was named as a new genus and species by William Healey DALL in 1884 based upon specimens collected by Charles R. Orcutt in Mission Bay (formerly False Bay), San Diego County, California. It is doubtful if any semblance of the exact locality within Mission Bay that Orcutt visited still exists (see, for example: ORCUTT, 1919: 64; MORRISON, 1952, 1954, 1957; CHAPMAN, 1963). This note brings together an obscure and scattered literature, summarizes available ecological data, documents further localities, corrects a recent literature statement concerning *Chlamydoconcha*, and establishes type material. The range is extended north to Shell Beach, Sonoma County, California ($38^{\circ}25'20''\text{N}$; $128^{\circ}07'00''\text{W}$) and south to Punta San Pablo, on the Pacific coast of Baja California Norte ($27^{\circ}12'30''\text{N}$; $114^{\circ}28'50''\text{W}$).

The family Chlamydoconchidae, erected by DALL (1884, as the family "Chlamydoconchae"; not 1889 (ABBOTT, 1974) and not 1899 (KEEN, 1969), in which *Chlamydoconcha* is placed, has been used by most American workers (KEEP, 1904, as Chlamydoconchidae; OLDROYD, 1925; KEEP & BAILY, 1935; BURCH, 1944; SMITH & GORDON, 1948; KEEN, 1969; KEEN & COAN, 1974; ABBOTT, 1974). THIELE (1934) regarded it as a subfamily (Chlamydoconchinae) of the Erycinidae, perhaps influenced by the remarks of FISCHER (1887a, 1887b) and BERNARD (1897a, 1897b). GÖTTING (1974) placed *Chlamydoconcha* in the Leptonidae. Its placement in the Erycinidae or Leptonidae, however, is incompatible with current diagnoses of either family (see CHAVAN, 1969; KEEN, 1971). KEEN (1969) erected the superfamily Chlamydoconchacea, removing *Chlamydoconcha* from its placement in the Erycinacea (Leptonacea) (DALL, 1921; THIELE, 1934; KEEN, 1963; VOKES, 1967).¹

Studies on *Chlamydoconcha* have concerned its anatomy (DALL, 1884; FISCHER, 1887a; BERNARD, 1897a, 1897b), with brief remarks existing on its distribution and natural history (WILLIAMS, 1949; TURNER & EBERT, 1962; TURNER, EBERT & GIVEN, 1969), and diet ("plankton," JOHNSON, 1953; "bacteria," TURNER & EBERT, 1962). Mentions by DALL, 1899, 1916; KELSEY, 1907; OLDROYD, 1925, and ORCUTT, 1885, 1900 and 1915b, cited occasionally in reference to *Chlamydoconcha*, are listings only, with no new information.

Table 1 summarizes the localities where *Chlamydoconcha* has been found. North of Point Conception, *C. orcutti* is known only from Sonoma and Monterey Counties. Previous Monterey records are old and few, without detailed information. In 1915, ORCUTT reported that, "A single specimen of this curious clam . . . is reported from Monterey bay, California." In 1919, ORCUTT wrote again "... since reported from Monterey Bay by Dr. [S. Stillman] Berry." The source of Berry's record, if first published by other than Orcutt (as Orcutt's wording would appear to imply), has not been located; *Chlamydoconcha* does not appear in Berry's checklist of Monterey Bay mollusks (BERRY, 1907, 1908). Whether DALL's (1921) citation is a repeat of Orcutt's listing cannot now be known. A second (or third) report from Monterey was that of Harold Heath of Hopkins Marine Station, of unknown date (SMITH & GORDON, 1948).

A single specimen recovered subtidally at Shell Beach, Sonoma County, in 1969 by a University of California at Berkeley zoology student was brought to the Bodega Marine Laboratory and examined by Dr. Cadet H. Hand, myself, and others. Unfortunately, the specimen was not retained.

Chlamydoconcha has been found from the littoral zone to a depth of 38 m, often clinging to and crawling upon the undersides of rocks. It may be restricted further in some areas to rock substrates over detritus-rich mud and sand bottoms (BERNARD, 1897b; TURNER & EBERT, 1963).

¹ The chiton genus *Chlamydoconcha* Pilsbry, 1893, a junior homonym, is a synonym of *Amicula* Gray, 1847 (SMITH, 1960).

Table 1
Records of *Chlamydoconcha orcutti*

Locality (Date, Collector)	Habitat	Authority, Depository
CALIFORNIA		
Sonoma Co.: Shell Beach State Park, 11.7 km north of Bodega Bay (17-V-1969)	sublittoral, about 9m ²	specimen examined at Bodega Marine Laboratory (not preserved)
Monterey Co.: Monterey Bay		ORCUTT, 1915a, 1919
Monterey Co.: "Monterey"		DALL, 1921
Monterey Co.: Monterey Bay: Pacific Grove	intertidal, on rocks	HEATH, <i>in</i> SMITH & GORDON, 1948; notes by Allyn G. Smith
Monterey Co.: Monterey Bay: Pacific Grove: Chase Reef (VIII.1971, A. J. Ferreira)	under rock, 15 m	CASIZ
Monterey Co.: Monterey Bay: off Monterey (6.VIII.1970, A. J. Ferreira)	under rock, about 30 m	MLML (no. M0013)
Monterey Co.: Carmel Submarine Canyon	on rocks, about 24 m	J. H. McLean (<i>in litt.</i>)
Santa Barbara Co.: Santa Barbara		JOHNSON, 1953; TURNER, EBERT, & GIVEN, 1969
Santa Barbara Co.: Hope Ranch Beach (10.XI.1967, S. Spaulding)	kelp holdfast	SBMNH (no. 25073)
Channel Islands: Santa Cruz, Anacapa, Santa Catalina, and San Clemente	under rocks, 3 to 38 m	TURNER & EBERT, 1962; TURNER, EBERT, & GIVEN, 1969
Los Angeles Co.: Santa Monica Bay	crawling on rock under-sides and stones in detritus-rich sandy-mud areas; to 18.3 m; 7 to 10 specimens under a single small flat rock	TURNER & EBERT, 1962; TURNER, EBERT, & GIVEN, 1969; UCMP; LACM; USNM (no. 576192)
Orange Co.: Newport Bay (1929, Lowe; others, no date)		E. M. & E. P. CHACE; M. CARUTHERS; H. LOWE, all <i>in</i> BURCH, 1944
San Diego Co.: La Jolla: Bird Rock (16.VIII.1927, P. Barnhart)		Williams, 1949; CASIZ (no. G-32760)
San Diego Co.: San Diego: Point Medanos (near entrance to Mission Bay) (I.1948, W. Williams)		CASIZ (no. G-32759)
San Diego Co.: San Diego: Mission Bay (False Bay)	on the shore, anchored by a byssus to under sides of stones; on a muddy, stony bank and stony clam bed; under rocks	Dall, 1884; Orcutt, 1885; Bernard, 1897b; Orcutt, 1915a; the Chaces, <i>in</i> Burch, 1944; Johnson, 1945; Williams, 1949; USNM (nos. 107222-107234; 758567-758568); CASIZ (no. G-32761; 27.IX.1946, W. Williams)
San Diego Co.: off Imperial Beach (9.X.1946, E. W. Scripps, Kenyon, Williams)	dredged on kelp; rocky bottom with heavy algal growth	WILLIAMS, 1949; CASIZ (no. G-32758)
BAJA CALIFORNIA NORTE, MEXICO		
Isla Cedros Island (ca. 1930s)		Walter Eyerdam collection (Frank Bernard, <i>in litt.</i>)
Punta San Pablo (25.X.1971, R. V. Searcher, J. H. McLean, P. LaFollette)	rocky pinnacles off point, sand base, strong surface current, 21-30 m	LACM (no. 71-178)

In Santa Monica Bay, it has been observed in the fall and winter (August to January, with occasional individuals in April), reaching population peaks about October (TURNER, EBERT & GIVEN, 1969). It has also been recorded in April at Santa Catalina Island (TURNER & EBERT, 1962). All other records (Table 1) are based upon fall and

winter collections (August, October, November or January) with the exception of the Shell Beach specimen, found in May. Two records are from kelp or kelp holdfasts (Santa Barbara and San Diego Counties), both also associated with rock bottoms. WILLIAMS (1949) stated *Chlamydoconcha* was found beneath rocks, cling-

ing to dead shells of old rock oysters, *Chama* sp., but did not indicate a specific locality. NORTH (1976) described it as occurring "beneath flat rocks and ledges," to depths of 27 m, in southern California. Its principally inner sublittoral occurrence and its rarity in the intertidal zone may account for the relatively few records.

In 1974, SOLEM (pp. 81-82) made the following statement: "Until recently it was believed that a genus of clams found off Western North America, *Chlamydoconcha*, was a permanently swimming member of the plankton, with completely internal shell. A study issued early in 1973 concluded that this genus was based on exceptionally long-lived larvae. It is not yet known to which adult clam these larvae belong, but the absence of any reproductively mature examples of *Chlamydoconcha* strongly suggests that this conclusion is correct." These remarks actually concern the North and South Atlantic galeommatacean clam *Planktomya* (see ALLEN & SCHELTEMA, 1972). *Chlamydoconcha* has never been recorded in the plankton or as a planktonic animal, and reproductively mature specimens are known (BERNARD, 1897b).

The type series of *Chlamydoconcha orcutti*, not located at the time of preparation of the catalogue of Dall's taxa (Boss *et al.*, 1968) has since been found in the National Museum of Natural History (Smithsonian Institution) wet (alcoholic) collections. This material (old alcoholic series no. 2015) consists of a bottle, with a neck-label reading "San Diego C. R. Orcutt," in which are 4 vials. One vial contains one dissected specimen and one entire specimen (the latter here designated the lectotype, USNM 758567, 10.1 mm in length and 9.4 mm in width; the former, a paralectotype, here designated, USNM 758568). A second vial contains 5 entire specimens (paralectotypes, here designated, USNM 758568). Two small vials contain shell fragments from the dissected specimen. The arrangement of the material into one dissected specimen, shells, and whole specimens, clearly corresponds with Dall's original remarks and description of the species. In addition, there are 7 slides (J125-J131, USNM 107222-107234) of one entire animal which has been serially sectioned. The catalogue entry (of October 16, 1894) indicates that this specimen was received from J. A. Ryder, and collected by C. Orcutt from False Bay (= Mission Bay). MOUNT (1973) has indicated the presence of a syntype (which can now be regarded as a paralectotype) of *Chlamydoconcha* in the C. R. Orcutt collection now at the University of California at Riverside.

Specimens examined are at the University of California, Berkeley, Museum of Paleontology (UCMP), California Academy of Sciences, San Francisco, Department of Invertebrate Zoology (CASIZ), Moss Landing Marine

Laboratories, Moss Landing, California (MLML), Santa Barbara Museum of Natural History (SBMNH), the Los Angeles County Museum of Natural History (LACM), and the National Museum of Natural History [NMNH, numbers of the United States National Museum (USNM)].

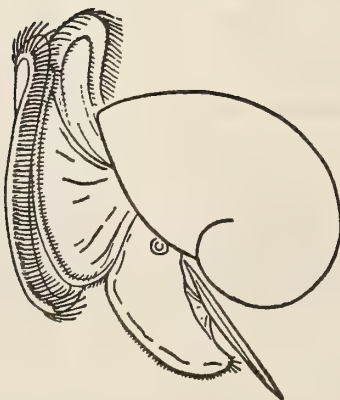
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Description of a Previously Misidentified Species of *Epitonium*

(Gastropoda : Epitoniidae)

BY

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(2 Text figures)

LONG CONSIDERED to be *Epitonium* (*Nitidiscala*) *barbarinum* Dall, 1919, a species common intertidally along the northern shores of the Gulf of California, Mexico, is in need of a new name. The confusion was caused by DALL's (1921: 116) range from San Diego, California to Panama. The holotype of *E. barbarinum* (USNM 46229), type locality San Diego, California, is a specimen of *Epitonium* (*Epitonium*) *angulatum* (Say, 1830), from the Atlantic seaboard and the Gulf of Mexico. A new name is chosen herein for the small species previously known as *E. (N.) barbarinum* Dall, 1919.

Epitonium (*Nitidiscala*) *arcanum* DuShane, spec. nov.

(Figure 1)

Description: Shell small in size, white; nuclear whorls 3, opaque, somewhat eroded even on live-taken material; subsequent whorls 5 to 7; spiral sculpture sometimes faint on first 2 whorls below the nuclear whorls; suture impressed but not deep; costae 13 to 17, very slightly reflected, thin-edged, heavier where they join the suture, sometimes slightly shouldered, dipping under the lip; aperture oval; lip entire, slightly patulous and without spine; operculum thin, horny, paucispiral. Length, 5 to 12 mm; width, 2 to 6 mm.

Type Material: Holotype, Los Angeles County Museum of Natural History, Type Collection no. 1264.

Paratypes: Four each will be deposited in the following institutions: American Museum of Natural History; California Academy of Sciences; Los Angeles County Museum of Natural History; Santa Barbara Museum of Natural History; United States National Museum. In addition, paratypes are in the collections of the following:

Twila Bratcher (2); Roy Poorman (2); Donald Shasky (4); Carol Skoglund (2); Helen DuShane (86).

Type Locality: Puertecitos, Baja California Norte, Mexico (30°20'02"N; 114°38'08"W), collected intertidally from algae covered boulders; from under rocks edging the sand beach; dredged to 18 m, shell and sand substrate. The range of this new species is restricted on the west side of the Gulf of California from San Felipe



Figure 1

Epitonium (*Nitidiscala*) *arcanum* DuShane, spec. nov.

Ventral view, holotype, LACM 1264; length 9 mm; width 4 mm

Table 1

Character	<i>Epitonium arcanum</i>	<i>Epitonium tinctum</i>	<i>Epitonium angulatum</i>
Number of whorls	8-10	7-11	9-10
Sculpture of early whorls	spiral in some specimens	smooth	smooth
Number of costae	11-17	11-14+	8-12
Shape of costae	blade-like	thick, coalescing into heavier costae near the lip	blade-like, definite angle at whorl shoulder
Size variation			
length	5-12 mm	4-15 mm	13-25 mm
width	2-6 mm	1-6.5 mm	6.5-9 mm
Suture	impressed, not deep	deep	deep
Color band at suture	none	brown line in some	none
Aperture	oval, patulous	oval, patulous	subcircular, lip held away from body whorl by costae, patulous

south to 20 km S of Puertecitos, Baja California Norte, Mexico, and on the east side of the Gulf of California from Cabo Tepoca south to Punta Peñasco, Sonora, Mexico, above latitude 30°N.

Discussion: *Epitonium (Nitidiscala) arcanum* differs from *E. (N.) tinctum* (Carpenter, 1865), with which it has been compared, by having a smaller shell, a different radula, and a different geographical range. Table 1 shows other differences.

The radula of *Epitonium arcanum* indicates that dentition is in the form of 20-40 broad rows of hook-like uncini with very little variation in shape along each row. The length of the teeth varies with the position of the teeth in the row, becoming progressively shorter with the distance from the center. The obtuse angles on the teeth are variable as to their precise placement. Radula and specimen of *E. arcanum*, from Puertecitos, Baja California Norte, Mexico, are at the San Diego Natural History Museum, San Diego, California (Figure 2). In *E. tinctum*, with which it has been compared, the tips of the teeth have a bifid structure unlike any other thus far reported.

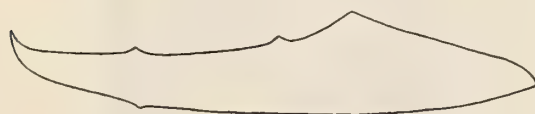


Figure 2

Epitonium (Nitidiscala) arcanum DuShane, spec. nov.

Radula: the hook-like uncini vary with their position in the row

The geographical range of *Epitonium arcanum* is in the Gulf of California, Mexico, above latitude 30° North. The range of *E. tinctum* is in the northeastern Pacific, from Bahía Magdalena, Baja California Sur, Mexico, north to Alaska.

Etymology: The specific name *arcanum* is derived from the Latin adjective *arcanus*, meaning "hidden," or "secret," referring to long hidden distinctiveness of this species.

ACKNOWLEDGMENTS

My thanks go to Dr. Myra Keen, Professor Emeritus, Stanford University for having read the manuscript and given helpful advice, and to Gale Sphon of the Los Angeles County Museum of Natural History for arranging the loan of type specimens. To Bertram Draper I am grateful for the photograph of the holotype of *Epitonium (Nitidiscala) arcanum*. I wish to acknowledge the extraction of the radula by the late Dr. George Radwin and the drawing of it by Anthony D'Attilio.

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Sexual Characteristics of *Margaritifera margaritifera* (Linnaeus) Populations in Central New England

BY

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(1 Text figure)

INTRODUCTION

BIVALVE MOLLUSKS are considered to be characteristically dioecious (gonochoristic) (COE, 1943). The few instances of consecutive or simultaneous hermaphroditism are believed to be chiefly confined to species in which larval or developing young are brooded in the gills or demibranchs of the parent (FRETTER & GRAHAM, 1964). Furthermore, it is generally found that species which are hermaphroditic are typically found in harsh or fluctuating environments. Both of the above conditions are characteristic of fresh water and tidal habitats.

Hermaphroditism has been explored in the Holarctic fresh water Unionacea by a few investigators (BLOOMER, 1934; TEPE, 1943; HEARD, 1970, 1975; VAN DER SCHALIE, several papers, summarized in 1970). These studies showed that fully hermaphroditic species were rare, although many species contained an occasional hermaphrodite. Populations of the Margaritiferidae, the most remote group morphologically within the Unionacea (ORTMANN, 1911; HEARD & GUCKERT, 1970), have been examined in Europe and North America. Studies by HENDLEBERG (1960) and VAN DER SCHALIE (1966, 1970), complete with summaries of earlier investigations, have indicated that *Margaritifera margaritifera sensu lato* is normally dioecious with only an occasional hermaphrodite being evident.

HEARD (1970) examined specimens of *Margaritifera falcata* (Gould, 1850) occurring in North American Pacific drainages. Finding all his material hermaphroditic, he concluded that *M. "falcata"* was hermaphroditic, thus proving an exception to the supposition of uniform unisexuality among the Margaritiferidae. However, VAN DER SCHALIE (1970) listed the locality of his own (1966) *M.*

margaritifera material (cited by HEARD, 1970) as occurring in the Snake River watershed in Wyoming. The Snake River drains the Pacific side of the Continental Divide and the *Margaritifera* inhabiting these waters is *M. m. falcata* (= *M. "falcata"*) (Henderson, 1935). Each study was on a single population sampled on a specific date. Assuming that van der Schalie's material was "*falcata*," it is uncertain whether *M. "falcata*," as a whole, is distinctly hermaphroditic, or dioecious with occasional hermaphroditism, although BURCH (1973) used hermaphroditism as a criterion distinguishing *M. "falcata"* from *M. margaritifera*.

The present study analyzes several populations of *Margaritifera margaritifera* inhabiting the Connecticut River system in central New England. Histological examination of the gonads was performed to determine sexual characteristics of these populations. Individuals of all ages collected at different times of the year were sectioned. Special attention has been paid to the distribution of sexes with respect to age, and to the possibility of sex reversal(s).

METHODS AND MATERIALS

A total of 52 specimens was utilized for visceral histological examination. All specimens were fixed in 10% formalin and preserved in 70% isopropyl alcohol.

The collections represent 13 populations occurring within the Connecticut River watershed in Massachusetts. A randomly collected sample, (MO. 896) Munn Brook, Westfield, Hampden County, of 18 specimens was used for sex ratio determination. All preserved material relevant to this study is maintained in the invertebrate collections of the Museum of Zoology, University of Massachusetts at Amherst.

Three specimens from a single locality (MO. 683) were selected for exploratory sectioning of gonads. All removed portions were embedded in paraffin and serially sectioned at $8\mu\text{m}$. Sections were then dehydrated in alcohol, cleared in xylene, stained and mounted with Pycolite. The serial sections were stained principally with Harris' hematoxylin and counterstained with eosin. Some material was stained with Ehrlich's hematoxylin. Fast green and acid fuchsin were also occasionally used as counterstains.

All parts of the gonad of each animal were removed and sectioned for examination for possible hermaphroditism. At least 25 slides, each consisting of about 4 sections, were prepared for each individual. This method was specifically employed in order to reveal rare tissues of an opposite sex in the same gonad, assuming that all animals were normally hermaphroditic. This criterion is based on HEARD's (1970) statement that, although *Margaritifera falcata* was normally hermaphroditic, male gonadal tissues were fewer than female.

At least 10 slides per animal were prepared for the remaining material except MO. 896 (18 specimens) and 7 follow-up specimens for which 5 slides per animal were prepared.

Ages of mussels 10 years and younger were determined by counting shell annuli, while older specimens' ages were determined by the application of growth curves developed previously for age analysis of Connecticut River system populations (SMITH, 1976).

RESULTS AND DISCUSSION

Histological analysis of the gonadal tissue of investigated mussels show that *Margaritifera margaritifera* in central New England is dioecious. Not a single case of hermaphroditism was disclosed. Inspection of gonads removed from specimens collected at different time intervals during the growing season (spring-fall), and including the recruitment period, did not reveal any follicular units undergoing sexual transformation, suggesting that individuals remain in a specific sex state during the warm season. It is not evident, however, whether an animal can undergo sex reversal at other times of the year nor if animals engage in sex changes at some particular period during their lifespan.

All inspected adult animals participated in the late summer - fall recruitment. Normal gametogenesis was observed from mid-May to early August after which spawning commences (SMITH, 1976). Sperm morulae, as

described and discussed by VAN DER SCHALIE & LOCKE (1941) and HEARD (1969, 1975) for other freshwater mussel species, were present in male follicles during June. By July all sperm morulae had disappeared and the acini were fully charged with mature sperm. Mature ova in females began appearing by mid-June and all acini contained fully mature ova during July. The histological evidence available during the spawning period indicates that females deposit eggs into the demibranchs prior to the release of sperm by males, suggesting that fertilization occurs after the eggs are in the demibranch marsupia. Following deposition of eggs, a few mature and immature oocytes remain in the ovary, however; these are apparently resorbed after a few weeks.

Identifiable sex cells are seen in animals between 7 and 9 years of age, whereas sexual maturity, as indicated by the ability to produce mature gametes, is not achieved for another year or so. The differences in time to reach sexual maturity appeared to be sex-dependent in examined mussels. Males apparently mature 1 to 2 years earlier than females (Figure 1). A female probably does not function reproductively until its 9th year, which is halfway through its normal lifespan of 19 to 25 years estimated by SMITH (1976) for populations in central New England.

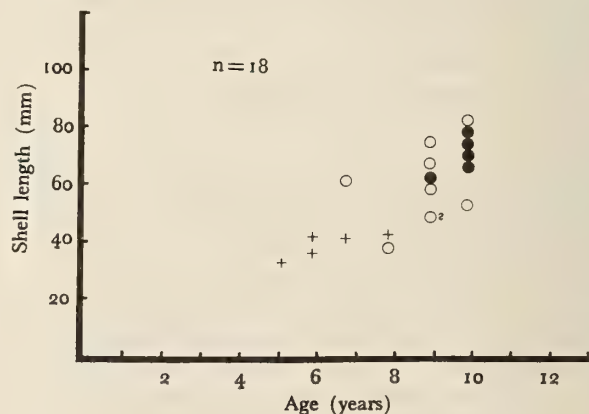


Figure 1

Distribution of juvenile and young adult specimens
+ - sex cells are unrecognizable ○ - males ● - females

Sexual maturity is gradual, as succeeding older mussels show greater amounts of gonadal tissue per unit area

of viscera. After mussels have become fully functional reproductives the correlation between the dominance of a particular sex and individual age disappears. Mature mussels of each sex are nearly equally distributed. Analysis of the Munn Brook population shows a moderate (5:3 or 23%) preponderance of females over males in the 9 to 15 year age category. This ratio slightly exceeds that given by PELSENER (1926) for several unrelated molluscan forms he studied. However, the dominance of females over males is in agreement with his observations. The available information does not indicate any protandric tendencies, although a slight male over female dominance existing in the pre-9 year old classes is replaced by a female over male dominance later on. Males are present in the older age classes of the Munn Brook population and among other examined specimens from many populations, large older males (> 100 mm shell length) are abundant.

The reasons for early male dominance followed by female dominance later on can not be explained by the available evidence and deserves further study. However, the appearance of males before females has been demonstrated for rhythmic and protandric hermaphroditic mollusks (COE, 1936). Early male preponderance has been suggested to be the result of bioenergetic economics wherein it is functionally easier or more economical to be male than female (RUSSELL-HUNTER & McMAHON, 1976).

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The Population Dynamics of Two Sympatric Species of *Macoma*

(Mollusca : Bivalvia)

BY

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(17 Text figures)

INTRODUCTION

THE ECOLOGY OF FEW intertidal deposit feeding bivalves has been studied. Variations in abundance have been studied for *Macoma balthica* for salinity (McERLEAN, 1964), tidal height (VASSALLO, 1969, 1971; GREEN, 1973) and substrate gradients (NEWELL, 1965) and for *Tellina tenuis* (STEPHEN, 1928) and *Scrobicularia plana* (HUGHES, 1970) for varying tidal heights.

Macoma secta (Conrad, 1837) and *M. nasuta* (Conrad, 1837) are geographically sympatric species of the bivalve family Tellinidae. *Macoma secta* occurs in intertidal sand flats from Vancouver Island, British Columbia, to Bahía Magdalena, Baja California, while *M. nasuta* occurs in muddier substrates intertidally from Kodiak Island, Alaska, to Cabo San Lucas, Baja California (COAN, 1971). RICKETTS, CALVIN & HEDGPETH (1969) list *M. secta* as occurring in the Middle Intertidal Zone and *M. nasuta* in the Low Tide Horizon. They are found in decreasing numbers to 25 fathoms [45 m] (ABBOTT, 1954). *Macoma secta* and *M. nasuta* are the characteristic species of the *Macoma* community on the west coast of North America. THORSON (1966) identified 5 *Macoma* communities worldwide.

Descriptive distribution ecology has been studied for *Macoma secta*, *M. nasuta* and 2 other *Macoma* species in relation to substrate (ADDICOTT, 1952). The present study is concerned with the population ecology of *M. secta* and *M. nasuta* as insight to comparative life history strategies. Population dynamics studied include population struc-

ture, spatial and temporal abundance patterns, population variability with tidal height, fecundity, recruitment and evidence of density dependence.

MATERIALS AND METHODS

Macoma secta and *M. nasuta* occur in sympatric populations on a sand flat known locally as Lawson's flat. This area is located 1.28 km from the entrance to Tomales Bay, just south of Dillon Beach, California. On the basis of an extensive stratified random survey of clam abundances with tidal height in June, 1974, at Lawson's landing, an area was staked out for future study. The area started at the 0.0 tide level and continued shoreward to the uppermost limit of distribution of *Macoma*. This upper limit is coincidentally obvious to the eye because the soil topography changes. This is due to biogenic working of the substrate above the area. There is also a 5 cm "cliff" at this transition zone. On surveying this "cliff" at various points on the beach, it was determined as 72 ± 3 cm from mean lower low water (MLLW). This corresponds to MLHW, one of DOTY & ARCHER's (1950) critical tide heights. The resulting area was 35 m long (perpendicular to shore) by 10 m wide. This was subdivided into 5 areas, each 7 m long by 10 m wide, for purposes of stratified random sampling along the tidal gradient.

In order to examine changes in abundance and size distributions with time and intertidal position, the clams were sampled every 2 months from August, 1974, to August, 1975. Three random samples were dug in each area. A 50 cm \times 50 cm frame was used and the holes were dug to a depth of ca. 70 cm in order to include all clams. The resulting pile of sand was searched twice by crumbling

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the soil in the hand. All clams were identified, counted and measured for length to the nearest millimeter. They were then returned to the hole which was refilled. It is felt that this method is accurate for clams of 1 cm and larger.

Distributional data on clams less than 1 cm long were obtained by monthly sampling of the 5 areas with the exception of biweekly sampling for a period of time after first recruitment. Ten cores (diameter 7.3 cm \times 11.0 cm long) were taken at random from each area and later sieved with a 1 mm sieve. The time and intensity of recruitment was also determined by this sampling procedure.

Estimates of fecundity in *Macoma* are difficult to obtain by usual methods. The bivalves will not readily spawn in the laboratory and since the gonads are impossible to excise accurately, they cannot be weighed. In order to obtain estimates of fecundity, samples were collected for each species in February and August, 1975. On the basis of histological study of the gonads (RAE, 1975) these times represented, respectively, the inactive and ripe phases of gonad sexuality. The hypothesis to be tested was whether or not the clams changed weight from winter to summer beyond that attributed to growth alone. Basic to this study was the assumption that any increase in weight disproportional to length was due to the added biomass of gametes. In order to obtain this estimate, each clam was numbered and measured for length with vernier calipers to 0.1 mm. Each individual's dry weight was obtained using only the soft tissue which was desiccated in an 80°C oven until constant weight was achieved. THORSON (1957) indicated dry weight yields better biological data than wet weight. Lines were fitted to the resulting length-weight data points and compared.

Size frequency data for the months August, 1974, February and August, 1975 were used to estimate the standing biomass in dry weight for each species at times when the populations were inactive and ripe with respect to gametogenesis. Shell lengths were converted to grams dry weight by the length-weight relationships outlined above for the respective months. The weight was multiplied by the clam abundance in each size class and all weights were summed. The resulting value was adjusted to a final value of dry weight in grams per m².

The phoronid, *Phoronopsis harmeri*, was also sampled bimonthly because it has been demonstrated to affect *Macoma* densities (T. Ronan, personal communication). Five random samples were taken in each area with a 10 cm \times 10 cm frame. In lieu of digging, the "burrows" were counted for an estimate of abundance. Counts were taken during calm weather so that wave action would have minimal effect on the "burrows."

The tidal height of each area was determined by surveying. On an expected tide of -24 cm with a barometric reading close to 750 mm and no wind blowing, a stake was driven into the mud at the point of furthest tidal retreat. This height was then double checked against a later -24 cm tide and points were subsequently surveyed.

Cursory sand analysis was performed in July, 1975 when one small core (3.3 cm diameter by 6.3 cm long) was taken from each area. The core was weighed wet and then weighed dry after desiccation in a 110°C oven. The samples were then gently broken up by mortar and pestle and dry sieved in a dry sieve series for 15 minutes. Resultant fractions were weighed on a Torbol balance.

RESULTS

Study Area

The slope of the beach was slight, averaging only 2.0%. There was, however, a distinct change in slope between areas 2 and 3. The sediment appeared sandy above this point and muddy below. The mean particle size was fairly constant across the area at approximately 245 μ m. The percent mud ($> 4 \Phi$) by weight was less than 1% with the exception of area one which was 5.4%, resulting in

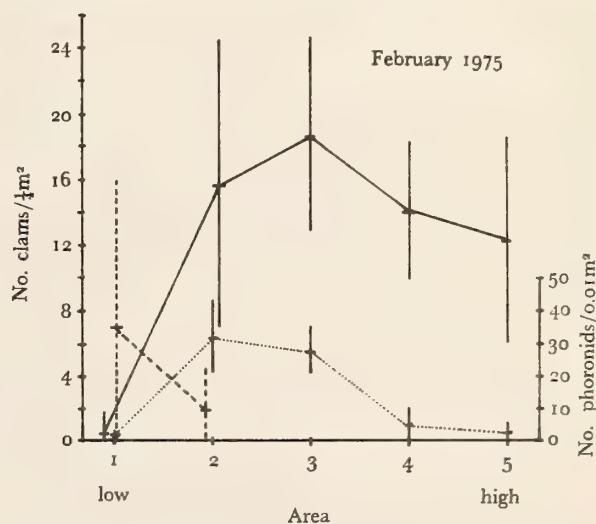


Figure 1

Mean abundances for each area for February, 1975
 (1) *Macoma secta* (—) (2) *Macoma nasuta* (---)
 number of clams per 0.25 m²
 (3) *Phoronopsis harmeri* (....) number of phoronids/0.01 m²
 Vertical bars represent 95% confidence intervals

the lower mean particle size of $224\text{ }\mu\text{m}$. The water content by weight was approximately 19.8% throughout the area.

Intertidal Distribution of Species

An example of the intertidal distribution of the species of interest is given in Figure 1. For *Macoma*, the mean abundance for each species is the average of the 3 samples taken in the respective area. For *Phoronopsis*, abundance is averaged from the 5 samples taken in each area. The month of February was a typical month. As will be shown later, the species were temporally stable in abundance.

Macoma nasuta is found low in the intertidal zone. The species was most abundant in area 1 where the substrate was muddy. Decreasing abundance in area 2 may be correlated with the less muddy substrate or it may mark the upper limit of the population's distribution. Throughout the sampling program, only 3 *M. nasuta* were found higher, one in area 3, one in area 5 and one above the sampling area.

The distribution of *Macoma secta* covered all 5 areas. In area 1, the counts were sparse but consistent; this probably marked the lower fringe. The greatest densities were found in areas 2 and 3. Abundance dropped in areas 4 and 5. The soil change, already described, marked the upper limit of *M. secta*'s distribution. Up to this boundary high densities were found and just above, no *M. secta* were ever found. This suggests adverse biotic relations with another species. Just above the boundary the ghost shrimp, *Callinassa californiensis*, was abundant. Both animals are deposit feeders, suggesting possible competitive exclusion. SEGERSTRÅLE (1965) reported a case where *Macoma balthica* and the amphipod *Pontoporeia affinis* had a strong inverse abundance relationship. He suggested predation of the *Macoma* larvae by the amphipod.

The distribution of *Phoronopsis harmeri* is important to the study of *Macoma* for several reasons. Dense beds of the phoronid have been known to smother *M. secta* entirely (T. Ronan, personal communication). Lesser densities may seriously hinder *Macoma*'s movements. As Figure 1 indicates, the phoronid's distribution closely approximated *M. secta* in range and area of peak abundances.

Shell length data for *Macoma* collected in February, 1975 are presented in Figure 2. Because the mean shell length of the *M. nasuta* population is rather variable with time, February data are not typical. It will be shown that this month is highly typical of *M. secta*, however. The largest individuals were found in areas 1 and 5, while areas 2 and 3 had consistently smaller clams. Two

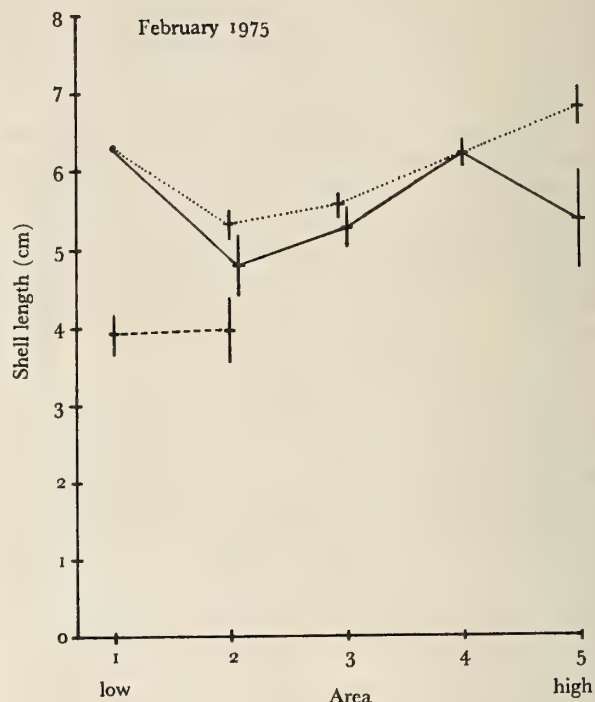


Figure 2

Mean shell length for each area for February, 1975
 (1) All *Macoma secta* (—) (2) Adult *M. secta* (. . .)
 (3) All *Macoma nasuta* (- - -)
 Vertical bars represent 95% confidence intervals

curves are shown for *M. secta*; the higher one does not include the young of the year, which were never abundant, but their small size statistically masked the intertidal size distribution of the adults.

Spatial and Temporal Changes in Population Ecology

Macoma secta

The change in mean density with time is presented in Figure 3. The grand mean cuts through all 95% confidence intervals. The extreme stability of mean abundance is indicated by the fact that the grand mean passes between 6 of the 7 50% confidence intervals. Analysis of

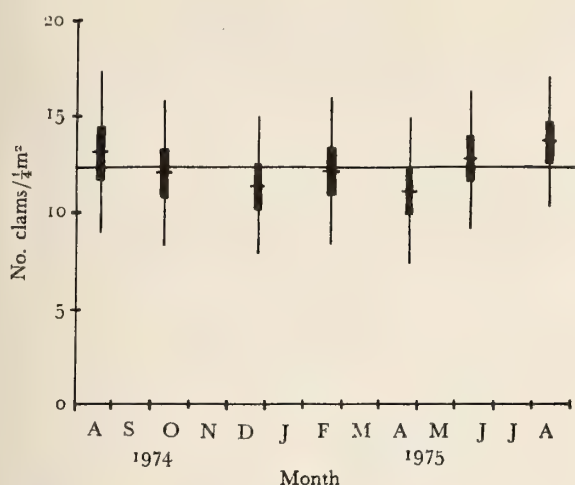


Figure 3

Overall mean abundance per 0.25 m² for *Macoma secta*. Thin vertical bars represent 95% confidence intervals; thick vertical bars represent 50% confidence intervals. Grand mean is also shown

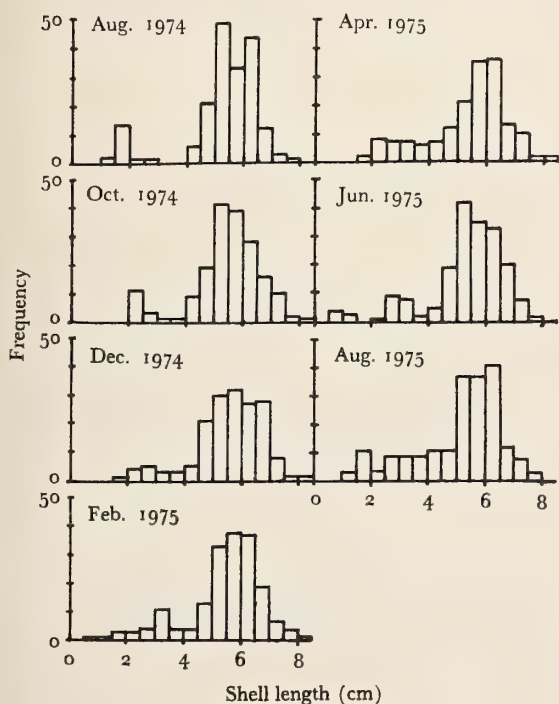


Figure 4

The size frequency distribution for *Macoma secta* remained rather stable. June, 1975 illustrates the 0+, 1+ and adult groups

variance indicated no significant changes in mean density ($F_{(6, 98 \text{ df})} = 0.288, p > 0.75$).

The population was rather stable in size composition. It was a bimodal distribution until June, 1975 when it became a trimodal distribution (Figure 4). The adults formed the largest mode and the 1 or 2 smaller modes represented the youngest age groups (0+ and 1+, respectively). To test for changes in size frequency distributions, the non-parametric Kolmogorov-Smirnov test was used. The size distribution for each sampling time was tested against all other times. Results are presented in Table 1 (SIEGEL, 1956, table M for large samples). Out of 21 comparisons, only 2 (10%) were significant at the 0.05 level. This is due to the 0+ group attaining a size of 1 cm in August, 1975.

Changes in mean length are summarized in Figure 5. The mean length ranged from 5.0 to 5.5 cm and analysis of variance showed these changes to be significant ($F_{(6, 1290 \text{ df})} = 2.60, p < 0.025$). ANOVA was repeated excluding the August, 1975 data and changes in size were not significant ($F_{(5, 1086 \text{ df})} = 1.059, 0.5 > p > 0.25$). This conclusively indicates the influence of the 0+ group on population length in August, 1975, the recruiting period.

Analysis of variance for the spatial-temporal analysis of abundances is given in Table 2. As shown, changes in

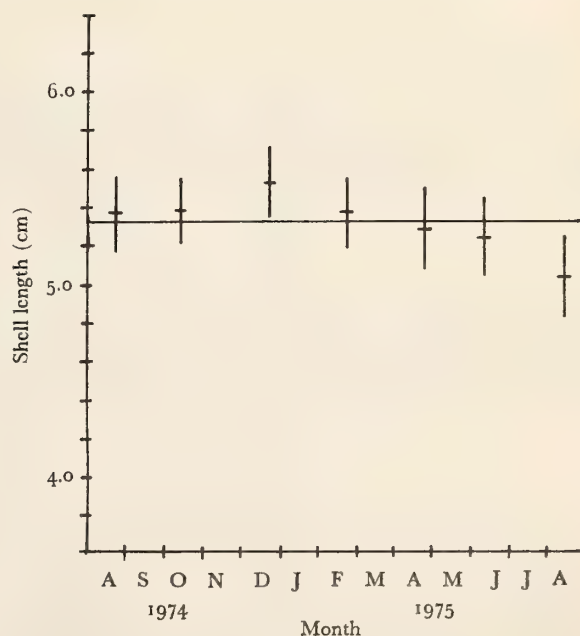


Figure 5

Mean shell length for *Macoma secta*. Symbols as in Figure 3

Table 1

Macoma secta—Kolmogorov-Smirnov test results

		1974 Aug.	Oct.	Dec.	1975 Feb.	Apr.	Jun.	1975 Aug.
1974	Aug.	—						
	Oct.	ns	—					
	Dec.	ns	ns	—				
1975	Feb.	ns	ns	ns	—			
	Apr.	ns	ns	ns	ns	—		
	Jun.	ns	ns	ns	ns	ns	—	
1975	Aug.	*	ns	*	ns	ns	ns	—

Macoma nasuta—Kolmogorov-Smirnov test results

		1974 Aug.	Oct.	Dec.	1975 Feb.	Apr.	Jun.	1975 Aug.
1974	Aug.	—						
	Oct.	ns	—					
	Dec.	ns	ns	—				
1975	Feb.	ns	ns	ns	—			
	Apr.	*	*	*	ns	—		
	Jun.	ns	ns	*	ns	ns	—	
1975	Aug.	*	*	*	*	*	ns	—

*—Significance at 5% level.

ns—Non significance.

Table 2

Model II 2 way Analysis of Variance for the spatial-temporal analysis of abundances for *Macoma secta*.

Source	df	SS	MS	F _s	Probability
Subgroups	34	3893.96	114.53		
A (areas)	4	3562.53	890.63	84.10	p << 0.001 ***
B (times)	6	77.16	12.86	1.21	0.50 > p > 0.25 ns
A × B	24	254.27	10.59	1.31	0.25 > p > 0.10 ns
Within Subgroups	70	564.00	8.06		
Total	104	4457.96			

Table 3

Model II 2 way Analysis of Variance for the spatial-temporal analysis of abundances for *Macoma nasuta*.

Source	df	SS	MS	F _s	Probability
Subgroups	13	298.310	22.95		
A (areas)	1	197.167	197.17	31.4	p < 0.005
B (times)	6	63.476	10.58	1.68	0.50 > p > 0.25
A × B	6	37.667	6.28	1.35	0.50 > p > 0.25
Within Subgroups	28	130.667	4.67		
Total	41	428.976			

abundance were highly significant ($p < 0.001$) for tide levels, but changes were nonsignificant with time. In addition, there was no tidal level \times time interaction.

Macoma nasuta

Changes in the mean density of *Macoma nasuta* per $\frac{1}{4}$ m² are shown in Figure 6. Stability in abundance is demonstrated since the grand mean intersects all 95%

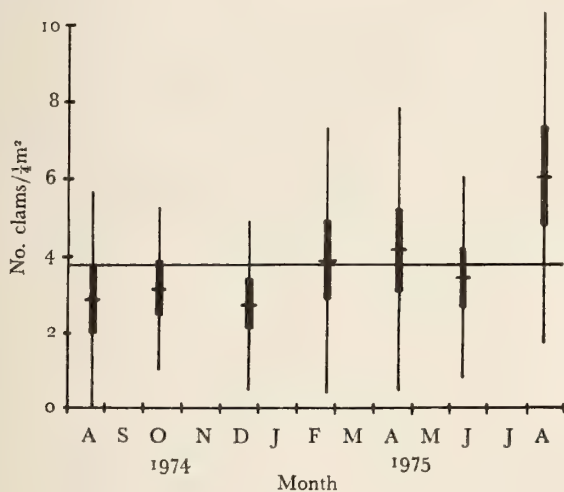


Figure 6

Overall mean abundance per 0.25 m² for *Macoma nasuta*. Symbols as in Figure 3

confidence intervals. Density appears more variable than in *M. secta* however, since the grand mean passes through only 4 of the 7 50% confidence intervals. Analysis of variance showed that differences between means were not significant ($F_{(6,42 \text{ df})} = 0.781$ $0.75 > p > 0.5$).

This clam has a rather variable size frequency distribution with time in comparison with *Macoma secta*. In June and August there was great influx of the 0+ group indicating recruitment. The Kolmogorov-Smirnoff test (with adjustments for small samples: MILLER & KAHN, 1962, appendix G) was used as before (Table 1). Of 21 comparisons, 9 were significant (43%). This is in part due to recruitment. Note the apparent lack of success of recruitment in August, 1974 (Figure 7).

The mean size of *Macoma nasuta* varied greatly in time (Figure 8); in this case from 3.1 - 4.4 cm. Temporal differences in means were highly significant (ANOVA $F_{(6,176 \text{ df})} = 8.49$ $p < 0.001$).

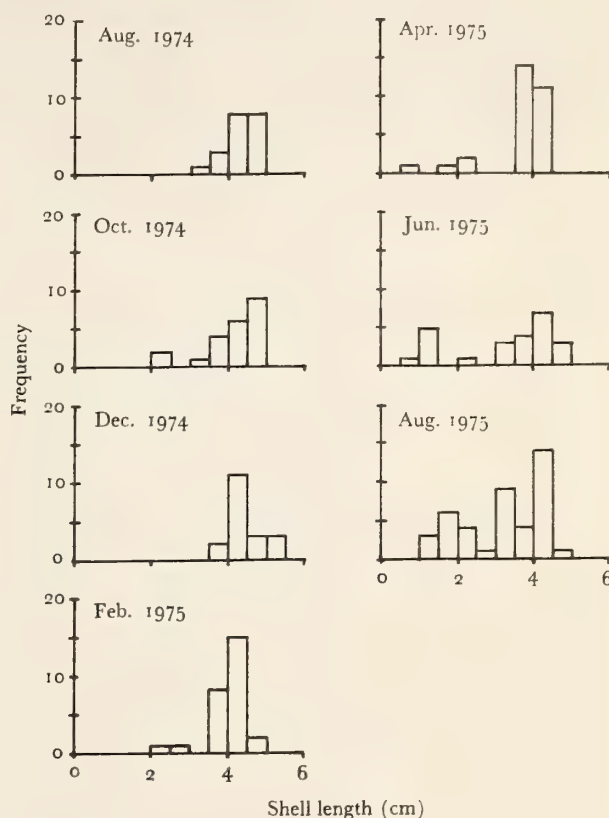


Figure 7

The size frequency distribution for *Macoma nasuta* for June, 1975. The recruits (0+), 1+ and adult groups are easily detected

Two way ANOVA was performed on the distribution data and is given in Table 3. The abundances differed with tidal height ($p < 0.005$), but there were no differences in abundance with time and there was no significant interaction.

Population Variability with Tidal Height

It has been proposed that environmental variability and population variability are strongly correlated, as suggested by GREEN (1969) who postulated that population abundances would show more variability in the higher intertidal areas where greater environmental unpredictability is thought to exist. Green's measure of popula-

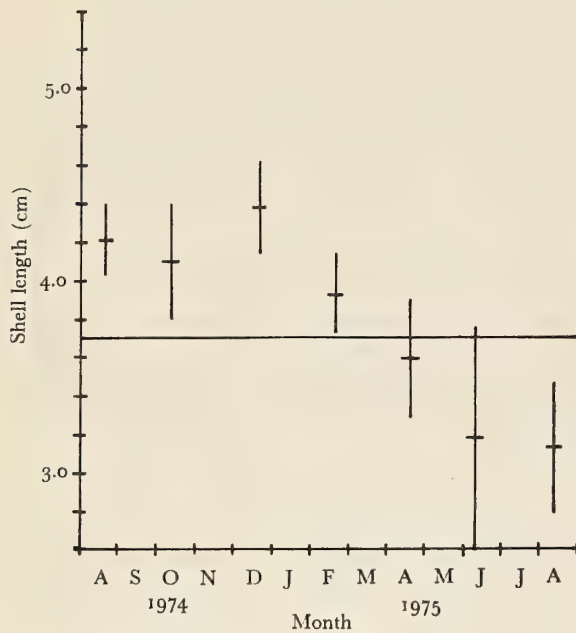


Figure 8

Mean shell length for *Macoma nasuta*. Symbols as in Figure 3

tion variability was the Population-Time Mean Square which is that portion of the variance from analysis of variance which is attributable to differences from time to time (the Among Means MS). This is plotted on a logarithmic scale against tidal height.

The Population-Time MS's for *Macoma secta* and *M. nasuta* are plotted in Figure 9. Regression of Population-Time MS against tidal height for *M. secta* was not significant ($t(3 \text{ df}) = 0.255$ $0.9 > p > 0.5$). This suggests that the environmental variability was the same for the clam at each tidal height. Since *M. secta* burrows deeply into the substrate, they may occur in upper areas but not be appreciably affected by surface environmental conditions. The clams burrow as deeply as their siphons are long (S. Obrebski, personal communication; ADDICOTT, 1952) and consequently the larger clams may burrow deeper. As Figure 2 showed, the larger clams were found higher up in the intertidal zone and consequently deeper in the substrate. The effect, then, is to escape the environmental variability of the soil surface by adding a thermal and saline buffer of soil between the clams and the surface. That larger clams are found higher in the intertidal zone may be a range extension mechanism.

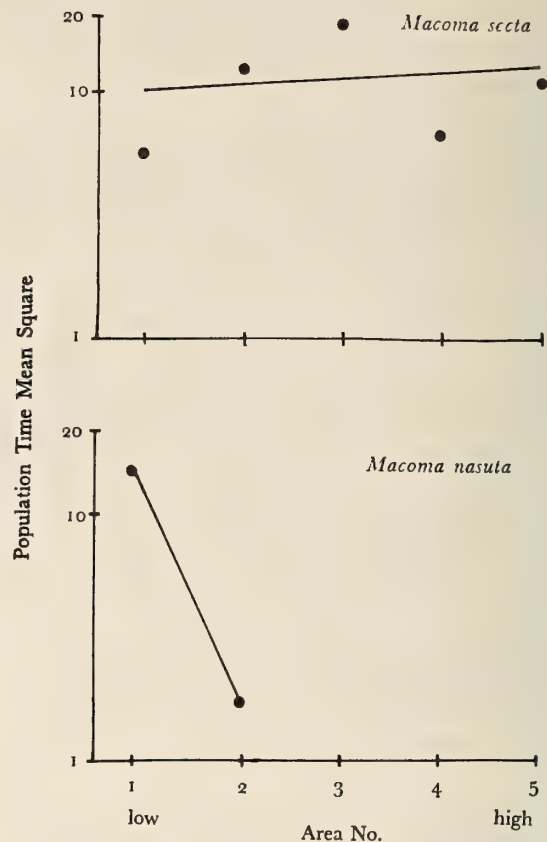


Figure 9

Population Time Mean Square with tidal height for *Macoma secta* and *M. nasuta*. Relation shown: $y = 0.49x + 9.6$. Ordinate on logarithmic scale

As only 2 data points are available for *Macoma nasuta*, comprehensive analysis is not possible; however, the value of the Population-Time MS for area 1 is high as compared with the *M. secta* data and especially high when compared to the intertidal animals GREEN (1969) discusses. GREEN (1968) found a similar high stress situation for the Mactrid bivalve, *Notospisula*, at lower levels, which was due to skate predation.

Fecundity

GALTSOFF (1961) indicated that *Macoma* (probably *M. balthica*), has a low fecundity. Our estimates of fecun-

dity in *M. secta* and *M. nasuta* started by examining their length to dry weight relationships in the inactive and ripe stages of gametogenesis and comparing them. These relationships are presented in Figures 10 and 11.

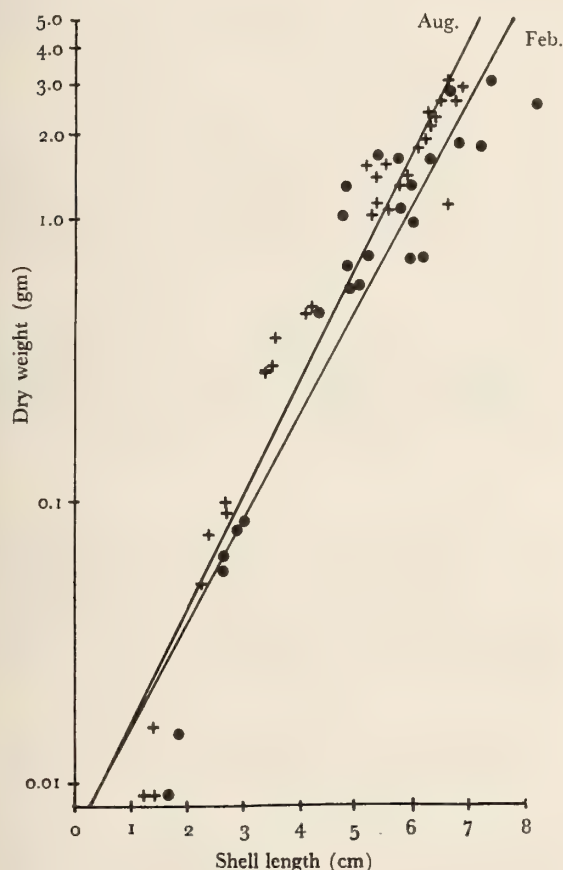


Figure 10

Dry weight (g) against shell length (cm) for *Macoma secta* for February 20 (inactive) and August 10 (ripe). Ordinate on logarithmic scale. February 20 (●) $\log n y = 0.844x - 4.951$; $r = 0.93$; $t(24 df) = 12.78^{***}$; $F_0(1, 24 df) = 163.37^{***}$; August 10 (+) $\log n y = 0.927x - 5.039$; $r = 0.97$; $t(28 df) = 21.75^{***}$; $F_0(1, 28 df) = 472.96^{***}$ (***) $p < 0.001$

All length-weight relationships for *Macoma secta* were highly significant ($p < 0.001$). The seasonal curves in Figure 10 were analysed by analysis of covariance. ANCOVA showed that the 2 lines are significantly different in intercepts ($F_0(1, 53 df) = 5.914$ $0.025 > p > 0.01$)

but not in the slopes ($F_0(1, 52 df) = 1.193$ $0.5 > p > 0.25$). The general indication from these curves is that *M. secta* did add weight in summer and, as assumed, mostly gametes. The added weight seemed to be 25 - 50% of winter weight. This is considerable, but probably small if compared to other bivalve species.

For *Macoma nasuta*, all length-weight relationships were also highly significant ($p < 0.001$). Analysis of

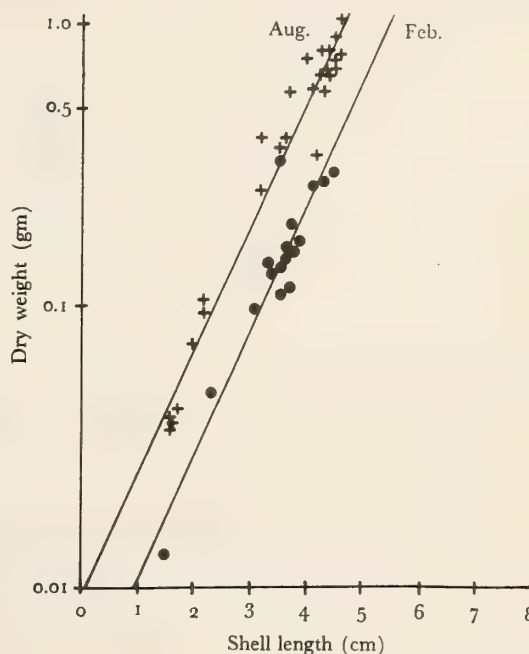


Figure 11

Dry weight (g) against shell length (cm) for *Macoma nasuta* February 20 (inactive) and August 10 (ripe). Ordinate on logarithmic scale. February 20 (●) $\log n y = 1.015x - 5.595$; $r = 0.98$; $t(15 df) = 18.14^{***}$; $F_0(1, 15 df) = 329.14^{***}$; August 10 (+) $\log n y = 1.008x - 4.670$; $r = 0.98$; $t(24 df) = 23.73^{***}$; $F_0(1, 24 df) = 516.65^{***}$ (***) $p < 0.001$

covariance on the seasonal curves in Figure 11 indicated that the lines differed significantly in intercepts ($F_0(1, 40 df) = 178.299$ $p < 0.001$), but not in slopes ($F_0(1, 39 df) = 0.0073$ $p > 0.75$). Consistent with general observations, *M. nasuta* gained a great deal in weight in gametes in the summer. The clams more than doubled their weight, adding about 125% of winter weight as gametes. This was much greater than *M. secta*'s seasonal weight increase.

Recruitment

Having made some estimates of reproductive effort, it is of interest to examine the timing and intensity of recruitment. Recruitment for both species was sparse during the time of study. The first recruits were discovered on January 22, 1975 for both species. On that date only 1 *Macoma nasuta* and 3 *M. secta* were collected. Their size ranged from 3.6 to 7.6 mm. Through May, the few recruits found were in this general size range. It is unknown why smaller individuals were not found.

By examining the reproductive data given in RAE (1975) and adding a probable 6-weeks larval stage, I would expect settlement of young to occur in October for *Macoma secta* and September, and from late October through late December for *M. nasuta*. The discrepancy between observed and expected times of settlement are not explainable at this time. For both species, the average number of recruits was 1 per 10 cores (each area), which equals 24 per m² in the areas of recruitment.

The *Macoma nasuta* recruits were found only in areas 1 and 2, the same as adults. The *M. secta* recruits were only found in areas 2, 4 and 5. These areas can quite confidently be called "nursery" areas. It is understandable that recruits of *M. secta* were not found in area 1 as it is a fringe area and muddy, but it is unknown why area 3 received no recruits. *Macoma secta* does move around a great deal in the substrate (S. Obrebski, personal communication), but evidently parallel to the shore. With only a very few exceptions, no young clams were ever found in area 3 when sampling for adults. This indicated that for 2 consecutive years, the "nursery" areas remained the same.

There was some evidence that juvenile mortality is high among settled *Macoma secta*. During January and early February, most recruits were found in areas 4 and 5. However, from February 20 on, few were found in area 4 and none in area 5. It is possible that the 32.5 cm of rain in the first 13 days of February so stressed the young that high mortalities resulted in the upper areas. For juveniles, this area is unpredictable, but for adults it is highly predictable.

Juvenile Growth

Macoma lives too deeply in the substrate and is difficult to sample, precluding mark-recapture studies of growth and survival. Previous attempts were unsuccessful (S. Obrebski, personal communication). The cohort of 0+ recruits could be detected in quantitative samples obtained in January, 1975. The growth of this cohort and the older 1+ group consequently could be followed in time since they were clearly distinguishable in size from

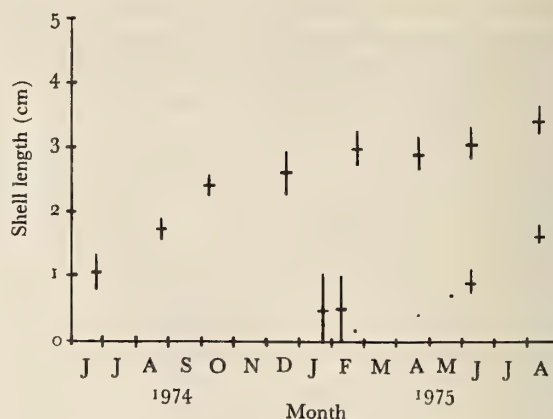


Figure 12

Juvenile growth of *Macoma secta* (0+ and 1+ groups shown)
95% confidence intervals shown

the rest of the population. Growth data for these cohorts are summarized in Figure 12. As the graph indicates, growth for these cohorts occurred throughout the winter, although it was slower at that time. For this reason, annual rings were not found on *Macoma* and data on age were unavailable.

Standing Biomass and Gamete Production

Macoma nasuta's biomass (dry weight g/m²) was 10.6 for August, 1974, 4.3 for February, 1975 and 10.3 for August, 1975. This seems to indicate for the survey year that the biomass remained rather constant from summer to summer. It also indicated the great amount of energy the population expended in gamete production (10.3-4.3 = 6.0 g/m²). This is $\frac{6.0 \text{ g/m}^2}{4.3 \text{ g/m}^2} \times 100\% = 140\%$ of winter weight expended in gamete production.

The biomass for *Macoma secta* (dry weight g/m²) was considerably greater, 89.9 for August, 1974, 54.2 for February 1975 and 77.6 for August, 1975. The biomass of *M. secta* was considerably larger than that of *M. nasuta* and was relatively stable from August to August. *Macoma secta* expended 77.6 - 54.2 = 23.4 g/m² in gamete production, 4 times that of *M. nasuta*, but only $\frac{23.4 \text{ g/m}^2}{54.2 \text{ g/m}^2} \times 100\% = 43\%$ of winter weight.

For comparison, McINTYRE (1970) obtained the range of biomass found for the *Tellina tenuis* community of

which that species is a major part. The range was 0.3 – 22.0 g/m² dry weight. Also, WARWICK & PRICE (1975) found the following values of biomass in dry weight averaged over the year: *Mya arenaria* 5.5 g/m²; *Scrobicularia plana* 2.1 g/m²; *Macoma balthica* 0.3 g/m² and *Cerastoderma edule* 0.8 g/m².

Density Dependence in *Macoma secta*

After examining the data on density and shell length of *Macoma secta* with tidal height (e. g., Figures 1 and 2) it became apparent that an inverse relationship existed between density and length for this population. The following analysis provides a strong argument for density-dependent growth in this clam.

Regression of mean shell length with mean density for each area sampled at different times was a significant ($p < 0.001$) inverse relationship as shown in Figure 13. The line plotted is only based on areas 2 through 5. This is done because area 1 was a fringe area, contained few

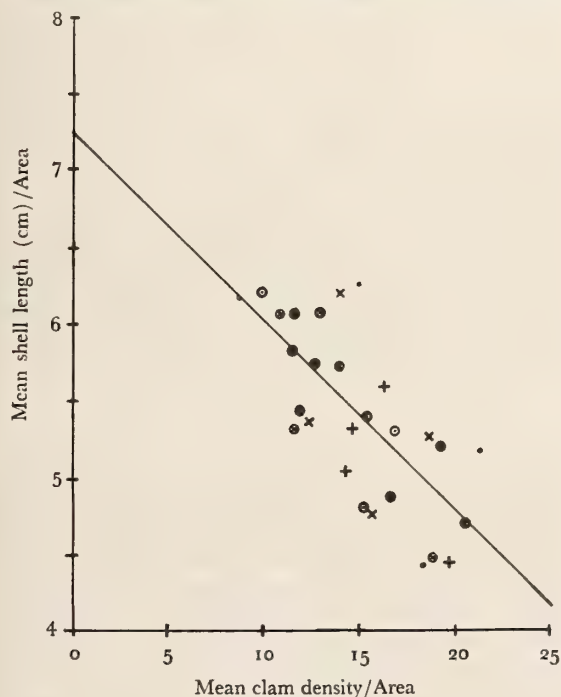


Figure 13

Mean shell length/area against mean abundance/area for *Macoma secta*

Equation for areas 2 to 5: $y = -0.1234x + 7.256$; $r = -0.72$; $t(26 \text{ df}) = 5.349^{***}$; $F_1(1, 26 \text{ df}) = 28.614^{***}$ ($*** p < 0.001$)
 • August 19 ○ December 23 ⊗ April 20 + August 10
 ● October 12 × February 22 ⊙ June 14

individuals and was not representative of the population. The following hypothesis was advanced. As density increases, the resources per individual decrease; therefore the growth rate of the individual decreases.

The hypothesis of density-dependent growth of individuals was tested on the easily distinguished 1+ group which was living in the nursery areas 2 and 5. Analysis of variance indicated that area 2 was significantly more dense than area 5 over the time interval ($p < 0.001$). The growth of this cohort in the 2 areas is shown in Figure 14.

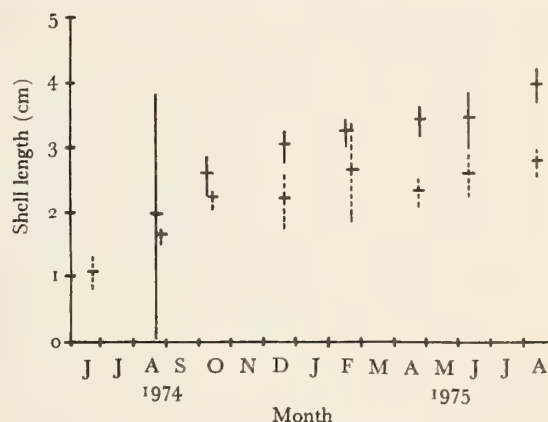


Figure 14

Mean shell length of *Macoma secta* juveniles from dense (area 2, dashed vertical) and sparse (area 5, solid vertical) populations. Vertical bars represent 95% confidence intervals

For each month following August, 1974, the means were significantly different. After 1 $\frac{3}{4}$ years of growth, the group in area 2 averaged 28 mm and the group in area 5 averaged 40 mm. Further evidence of the extent of density-dependent growth is seen in Figure 15 for August, 1975, a typical month. In areas 2 and 3 all modes are further to the left than in the less densely populated areas 1, 4 and 5. Even the largest mode, which was composed of several year groups, was distinctly affected.

It is of interest to know, for this population, what was the threshold density above which growth was negatively affected. To find this out, the cumulative length of clams found in each $\frac{1}{4}$ m² sample was plotted against its biomass in numbers. Cumulative length was found to be the best measure of biomass because weight changed seasonally to the degree where relationships would be masked. This is shown in Figure 16.

The 2 lines shown are (1) the calculated relationship, which assumes density-independent growth (dashed line),

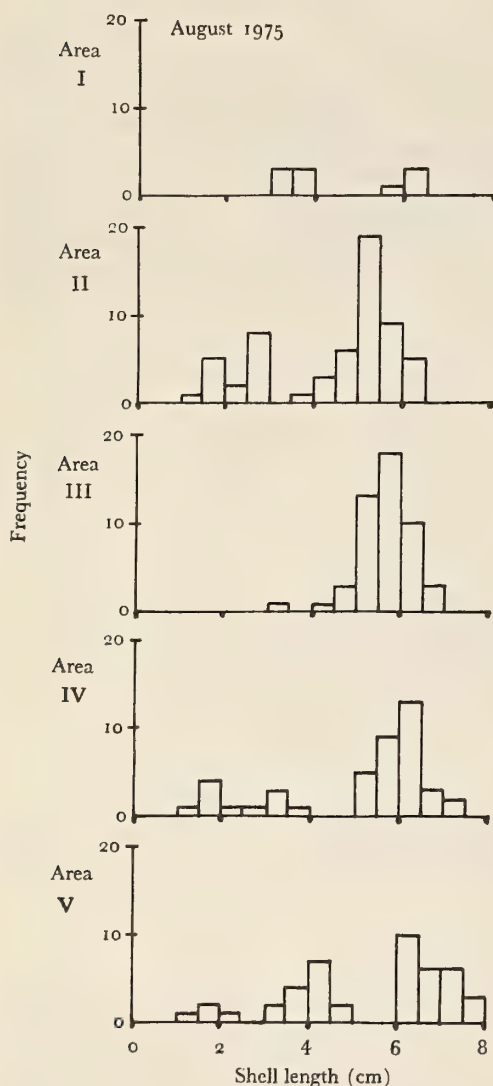


Figure 15

Size frequency distributions of *Macoma secta* for each area in August, 1975

in which the slope is the grand mean shell length of all clams collected and (2) the actual relationship of biomass (cumulative length) per 0.25 m² sample against the number of individuals in that sample ("density"), which shows density-dependence (solid line - regression of all points). Implicit in the calculated line showing density-

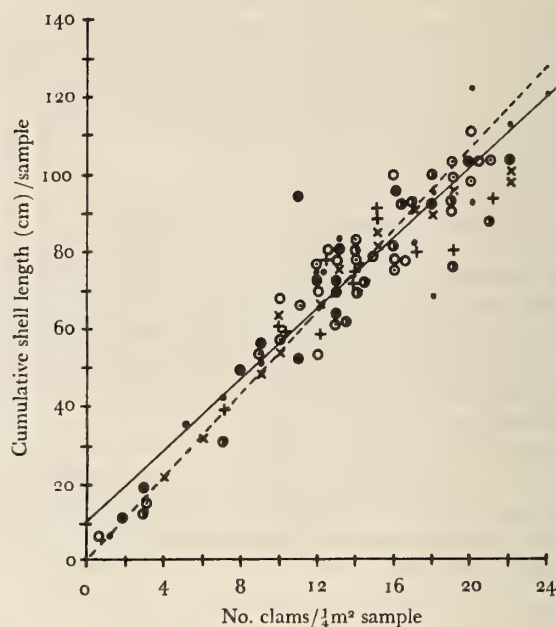


Figure 16

Biomass (cumulative shell length) with the number (abundance) of *Macoma secta* from each 0.25 m² sample.

Equations: density dependent relation (—). Calculated density independent relation (---). The slopes of the 2 lines were significantly different, t (92 df) = 4.245*** $p < 0.001$; calculated density independent relation $y = 5.319x$; density dependent relation: $y = 4.573x + 10.812$; $r = 0.94$; t (92 df) = 26.02***; $F_{(1, 92 \text{ df})} = 676.78$ ***. For each month sampled all relationships were highly significant; $p < 0.001$; $0.87 < r < 0.97$. Symbols as in Figure 13

independence is the assumption that the mean shell length for the whole population for all sampling dates is the same for a density-independent or a density-dependent population. The density-dependent relationship is highly significant ($p < 0.001$) and the slopes of these 2 lines were shown to be significantly different ($p < 0.001$). These lines intersect at a density of 14.49 clams/0.25 m². At that point density-dependence has no effect. At lower densities there is a relative abundance of food or space, or both, and at higher densities a crowded situation is found. As density increases, it is clear that the stress of reduced food and growth will result in a threshold density of emigration or mortality. Empirical data suggest this threshold was near 24 clams/0.25 m², as this was the highest density recorded.

Phoronopsis harmeri

In order to obtain an estimate of phoronid population dynamics a Two-way analysis of variance was run on the phoronid abundance data. The test indicated temporal stability of numbers ($F_6(6, 24 \text{ df}) = 2.22$ $0.1 > p > 0.05$) but differences in abundance with tidal height ($F_4(4, 24 \text{ df}) = 41.11$ $p < 0.001$). It also showed that there was a significant tidal height \times time interaction ($F_{24}(24, 140 \text{ df}) = 1.83$ $p < 0.025$). Perhaps this was due to totally unpredictable recruitment or mortality.

There was a similarity between *Macoma secta* and *Phoronopsis harmeri* in abundance patterns and tidal range. In Figure 17, the mean abundance of *M. secta* per

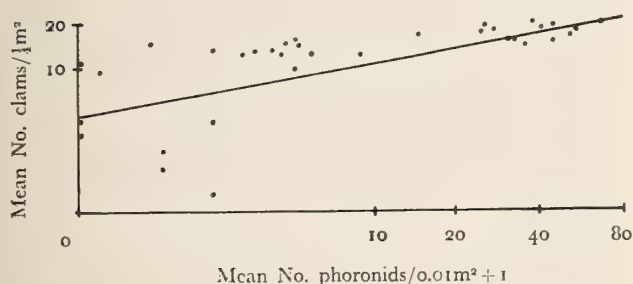


Figure 17

Mean abundance *Macoma secta* with mean abundance *Phoronopsis harmeri* for each area on each sampling date. Relationship: $\log n(y+1) = 0.3953 \log n(x+1) + 0.6720$; $r = 0.67$; $t(33 \text{ df}) = 5.7^{***}$; $F_6(1, 33 \text{ df}) = 26.73^{***}$ ($p < 0.001$). For graphic presentation $\log_{10} - \log_{10}$ scales are used

0.25 m^2 is plotted against mean abundance of *P. harmeri* per 0.01 m^2 for all areas and all dates. The logarithmic relationship is highly significant ($p < 0.001$). The distribution of the phoronid was highly contagious at the 0.01 m^2 level of heterogeneity (USHER, 1973). The variance to mean (s^2/x) ratio in most computations of abundance approximated 6. However, this was from a relatively sparse population. JOHNSON (1959) found that *P. harmeri* had an even distribution in very dense beds. Despite the positive correlation with *Macoma secta* I found, when very high densities of the phoronid were achieved, *M. secta* is driven out (T. Ronan, personal communication). This suggests that the data given may represent part of a parabolic relationship.

DISCUSSION

With the knowledge of the population dynamics and life histories of *Macoma secta* and *M. nasuta*, some interesting comparisons can be made. A synthesis of current information enables us to say that *M. secta* is mainly a deposit feeder, with little dispute (POHLO, 1967, 1969). However, *M. nasuta* has been considered a strict filter feeder (REID & REID, 1969) and a strict deposit feeder (HYLLEBERG & GALLUCCI, 1975; MCGINITIE, 1935; POHLO, *opp. cit.*). YONGE (1949) believed all tellinids to be deposit feeders. As a by-product of histological work describing the seasonal gonadal cycle for both species (RAE, 1975), I concur that adult *M. secta* are basically deposit feeders on sandy substrate. However, *M. nasuta* appears to be a facultative feeder. Throughout most of the year the gut is filled with amorphous organic matter and some clearly identifiable diatoms. This organic matter may have been ingested by deposit feeding, albeit highly selectively, or by suspension feeding on resuspended organic debris. E. H. Smith (personal communication) indicates *M. nasuta* will ingest carmine particles from the water column. However, in March, 1974 and March, 1975, the gut was primarily filled with sand. Possibly that time period produced the most stress on the animal, in terms of food availability and it resorted to deposit feeding on larger particles. RHOADS & YOUNG (1970) have indicated that active deposit feeders rework the fine substrates, increasing their water content in the process. Since the water content appeared stable throughout the sandy and muddy substrates, it is doubtful that any significant deposit feeding was occurring in mud where *M. nasuta* lived.

Suspension feeders typically inhabit sandy substrates and deposit feeders inhabit muddy substrates (RHOADS & YOUNG, 1970; LEVINTON, 1972); however, *Macoma secta* and *M. nasuta* were exactly the reverse. This may be explained in part by the supposition that for sympatric intertidal species the suspension feeder opts for the lower zone because of its dependence on the water column, irrespective of substrate while the deposit feeder necessarily is found higher on shore. The deposit feeder *M. balthica* is found in intertidal muds (NEWELL, 1965). Newell explained the clam's distribution on the basis of a heavy concentration of bacteria, a potential food, in the fine-grained deposits. *Macoma secta* must be highly evolved in its feeding style because of its occurrence in sandy sediments. In fact, it has been shown (E. H. Smith, personal communication) that *M. secta* has developed a mechanism to deposit feed while the tide is out.

With this in mind, the 2 species of *Macoma* may be compared as to population strategies. The *M. secta* population studied was characterized by stable abundances and size structure over a year's time. *Macoma secta* is of large size, has relatively low fecundity, low recruitment, low production/biomass ratio and is susceptible to density-dependent effects. LEVINTON (1972) made the statement that deposit feeders are usually more stable in abundance than filter feeders; *M. secta* dynamics further verify his idea. All the characteristics of this population fit the model of a biologically accommodated animal (SANDERS, 1969) living in a rather "mature" community (MARGALEF, 1963). These models represent the best attempts to date to understand the dynamics of an animal such as *M. secta* and how they relate to environmental fluctuations and evolutionary strategies.

Macoma nasuta can be given the same life history attributes as *M. secta* when compared to other benthic invertebrates; however, in comparison to *M. secta*, *M. nasuta* has attained modified population dynamics, possibly due to its partial dependence on filter feeding. This mode of feeding is characterized by irregular bursts of food availability. This instability is bound to affect the population (LEVINTON, 1972). Compared to *M. secta*, abundances and size structure are less stable and it has a higher fecundity, smaller size, higher production/biomass ratio, and lack of density-dependent effects. This is typical of an animal living in a harsher environment. Perhaps the stress was the food availability, but it may be part of a larger picture.

CASTENHOLZ (1967) proposed the idea that the intertidal zone can be more stable than the subtidal zone in regions lacking climatic extremes. This is exactly the opposite of the general view. However, in the mild climate of the Californian west coast, the intertidal animals may be more than prepared evolutionarily for local extremes in weather, whereas subtidal animals evolved as "biologically accommodated", such that a weather change may greatly affect them on a low spring tide. These "biologically controlled" communities may be more unpredictable. *Macoma* dynamics seem to agree with this idea. The *M. secta* population was stable in the mid tide horizon and the *M. nasuta* population was less stable in the low tide horizon. This is true despite the assertion that *Macoma* is infaunal. The majority of the *M. secta* population lives 40 - 70 cm deep in the sediment while the majority of *M. nasuta* apparently live in the top 10 cm with a large portion living just under the surface. The extreme spring tides of December and June are bound to affect *M. nasuta*. In addition, populations of both the high intertidal marsh snail *Batillaria attramentaria* (WHITLATCH, 1974) and the littoral fringe snail, *Littorina planaxis*, of

the rocky intertidal zone (SCHMITT, 1974), both west coast species, fit Castenholz' argument. Both possess the attributes of stable populations.

The phenomenon of size gradients with shore level for mollusks has been reviewed by VERMEIJ (1972). He generalized that for high intertidal mollusks, the largest individuals are found at the highest levels and for low intertidal mollusks the largest individuals are found low. There can be many factors responsible for these gradients. Principally he believes that shore level gradients in mortality for post larval prereproductives is the cause and that these individuals will respond by seeking a low mortality zone. It has been shown that *Gemma gemma* (GREEN & HOBSON, 1970) and *Macoma balthica* (GREEN, 1973) show size gradients because of faster growth based on higher temperatures in the upper intertidal zone. EDWARDS (1969) indicated that larger *Olivella biplicata* can better withstand desiccation and survive the harsher upper zone to which they migrate. This gradation in size may often reflect an effective range extension such that older, hardier animals can move to less dense fringe areas, thus evening out densities. However, in some cases it appears that density-dependent growth of individuals is the cause.

In the case of *Macoma secta*, the size gradient seems to be due to an inverse relationship of density and growth. The limiting resource is probably volume of soil in terms of food and not in terms of space. *Macoma secta* does not display obvious territoriality since it has a random dispersion pattern (S. Obrebski, personal communication). Density-dependence has often been studied in terms of regulation of population numbers through various mechanisms, including mortality (for benthic invertebrates see MILEIKOVSKY, 1974; THORSON, 1966). Density-dependent growth of individuals represents the alternative, where biomass (weight/area) is maintained at the carrying level of the environment but not at the expense of numbers of individuals. This may be more efficient for the species because in the event of a local catastrophic mortality, the remaining population would more quickly be able to restore biomass through growth than by recruitment. This resiliency would be useful to certain species.

SUTHERLAND (1970) explained that the size gradient for *Acmaea scabra* was probably due to density factors wherein food was the limiting resource. That energy flow equality was demonstrated for 2 populations (SUTHERLAND, 1972) further indicated this.

Certain conditions were necessary in order that density-dependent growth could be demonstrated. The densities in each area had to remain constant over the time period, and for best results the size-frequency structure had to remain the same. ANOVA showed temporal stability

in abundance in each area. There was also temporal constancy in the size frequency structure in toto (Figures 4 and 15) and for each area (RAE, 1975). The adult modes remained stable and the only obvious change was juvenile growth. Because each area had its own identifiable size-frequency "fingerprint," this indicates that migration perpendicular to shore was virtually non-existent (RAE, *op. cit.*). It was rather strange that individuals in the dense areas 2 and 3 did not migrate into the less dense areas. When *Macoma balthica* was found infected with trematodes, it was found to behave strangely in that it traveled just under the substrate surface (SWENNEN, 1969). BRAFIELD & NEWELL (1961) did not realize the cause but noticed that its tracks always looped about each other in the course of the day. They determined that the animals are constrained to maintain their position on shore by "homing," using the sun to navigate. Perhaps *M. secta* does likewise.

It could be argued that *Macoma secta* grew faster high in the intertidal zone because of higher sediment temperatures and consequent higher metabolism, such as for *Gemma gemma* (GREEN & HOBSON, 1970) and *M. balthica* (GREEN, 1973); however, this is probably not the case here. Those clams are found near the surface of the substrate and are subject to temperature changes, but *M. secta* is found from 40 - 70 cm deep. As JOHNSON (1965) pointed out, diurnal temperatures have little effect below 10 cm.

One last condition for demonstrating density-dependency was that the different growth rates could not simply reflect food density. *Macoma secta* is mainly a deposit feeder and the assumption was made that food density either remained the same or even decreased with increased tidal height. Preliminary findings (W. Evans, personal communication) indicate that the amount of food material adhering to sand grains does not change with tidal height and the amount of flocculant material actually decreases with increasing tidal height in the area studied.

Density-dependency appears to act in 2 ways on populations of *Tellina tenuis*. For a population similar to *Macoma secta* in terms of size gradient and densities, STEPHEN (1928, 1929) thought the rate of growth may be influenced by density. It also appears that the predation on the siphons of *T. tenuis* by plaice may be density-dependent (TREVALION, EDWARDS & STEELE, 1970). There was a threshold density of clams below which predation apparently ceased. High densities of the clam resulted in heavy predation rates which consequently resulted in possible lower fecundities. Energy for reproduction would be shunted to repair and of course the siphons are important organs in the acts of feeding and spawning.

One factor believed to influence differences in growth for *Strongylocentrotus purpuratus*, the purple sea urchin, is food availability. This factor has been shown to be inversely related to density (EBERT, 1968). This view, that the density of food resource determines rates of birth, death, consumption, growth and production has been modelled by BROCKSEN, DAVIS & WARREN (1970) and illustrated by empirical data.

SUMMARY

1. The upper limit of *Macoma secta* was abrupt at +72 cm, one of the critical tide levels (DOTY & ARCHER, 1950)
2. Abundance did not change seasonally for *Macoma secta*
3. *Macoma secta* possessed a stable size-frequency distribution composed of the 0+ or 1+, or both, group and a large adult mode
4. There was significant seasonal variance in mean size of *Macoma secta*. However, this was due to recruitment influence
5. For each of 5 contiguous areas, abundances of *Macoma secta* were stable seasonally, but varied significantly with tidal height
6. Abundances did not change seasonally for *Macoma nasuta*
7. *Macoma nasuta* was characterized by a rather unstable size-frequency distribution
8. There was a highly significant seasonal variance in mean size of *Macoma nasuta*
9. For the 2 lowest areas, abundance of *Macoma nasuta* showed seasonal stability but varied significantly with tidal height
10. A measure of seasonal population variability, the Population-Time Mean Square, was found to have zero correlation with tidal height for *Macoma secta*, meaning that environmental stress was the same for individuals at each tidal height. This is believed related to the gradient of clam size to tidal height
11. Population variability was high in area 1 for *Macoma nasuta*. This may be due to human disturbance, batray predation or to *Ulva* matting
12. Seasonal variations in weight to length indicate that *Macoma nasuta* has a high fecundity and *M. secta*'s fecundity is relatively low
13. Recruitment of rather large "spat" (ca. 5 mm) was detected in January for both species. The reason for an absence of smaller sizes is unknown
14. Recruitment was light for each species
15. Year round growth is indicated for juvenile *Macoma secta*. Growth is slower in winter

16. The standing biomass of each species is high compared to other bivalves
17. A size gradient with tidal height was shown for *Macoma secta*. The largest individuals were found higher on shore
18. An argument for density-dependence in *Macoma secta* is given with emphasis on individual growth and realized population fecundities
19. Analysis of population dynamics indicated that in comparison to *Macoma nasuta*, *M. secta* was more stable. This supports CASTENHOLZ' (1967) idea that where climates are mild, the intertidal communities (and hence member populations) are more stable than the subtidal communities
20. Phoronid abundance did not vary significantly with time but did vary with tidal height
21. A positive correlation of phoronid density with *Macoma secta* abundance was found

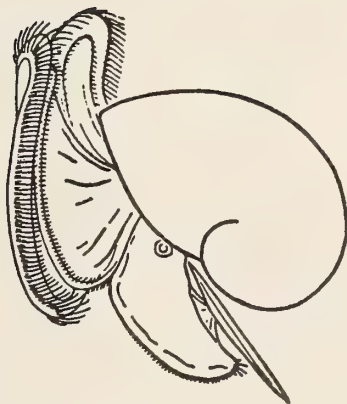
ACKNOWLEDGMENTS

I thank the members of my Committee, Dr. James Blake, Chairman, and Drs. Victor Loosanoff, Steven Obrebski and Edmund Smith, Director, for their help and encouragement throughout my study. Special thanks are due to Dr. Blake for reviewing the manuscript in its thesis form and Dr. Obrebski for his encouragement and ecological expertise in directing this research. My greatest thanks go to Susan for her help in the field, her encouragement and her typing skills.

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Notes on the Winter Epiphragm of *Pupoides albilabris*

BY

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(1 Text figure)

INTRODUCTION

DURING DORMANCY PULMONATE land snails typically occlude the aperture of the shell with one or more secreted partitions known as epiphragms (ROKITKA & HERREID, 1975). Although thin epiphragms are not highly impermeable (MACHIN, 1968; PICHER, 1972), the reduction of gas exchange across thick or multiple epiphragms can apparently be severe enough to require special provision for respiration. Many helicid epiphragms exhibit a distinct white patch or "Kalkfleck" opposite the pneumostome which may be an area of increased permeability (PICHER, *op. cit.*). Certain other pulmonates form well-defined slits or holes in each epiphragm (HORA, 1928; REES, 1964). This report describes the perforated winter epiphragm of *Pupoides albilabris* (C. B. Adams, 1841), a small land snail of the family Pupillidae. The observations refer to specimens collected from beneath stones and plant debris on a sparsely wooded slope in Lawrence, Douglas County, Kansas.

OBSERVATIONS

Winter-collected specimens possess a thick, brown hibernation epiphragm, very different from the thin, transparent film which is formed in other seasons. The epiphragm is remarkably tough yet flexible; treatment with acid indicates that it is not calcified.

The central portion of the hibernation epiphragm adheres to the surface beneath which the snail is sheltered. When detached from the substrate, the epiphragm remains intact in the aperture and the formerly attached portion is distinguishable by texture (stippled area of Figure 1A). Surrounding this central area is a narrow border unattached to the substrate. At the upper, outer margin of the aperture the border includes a well-formed

oval perforation. In 5 specimens, the mean dimensions of the pore were 190μ (161 - 219) by 104μ (88 - 117).

The inner surface of the hibernation epiphragm was examined after breaking away part of the first whorl of the shell behind the aperture (Figure 1B). The outer epiphragm is backed by a layer of very thin cells or bubbles of epiphragmal substance, which extends across the entire aperture. This secondary barrier is not perforated.

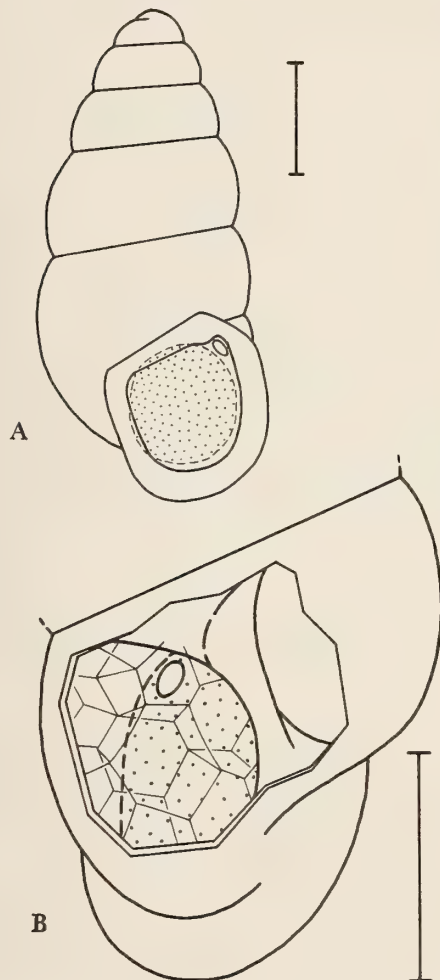
DISCUSSION

The classical view of the epiphragm as a hermetic seal preventing water loss (BINNEY & BLAND, 1869) is incorrect, as it is now known that water vapor diffuses fairly rapidly across intact epiphragms. The mantle collar tissue is the primary barrier to evaporation from the aperture and the vapor pressure gradient across the epiphragm itself is probably very low during dormancy (MACHIN, 1968). However, epiphragms are vital in water conservation since they protect the sensitive mantle collar and pneumostome from disturbance by small arthropods or wind-blown debris. Such disturbances would greatly increase mucus secretion and evaporative water loss (NOPP, 1974). The protective function could be especially im-

(on facing page →)

Figure 1

A. Dormant individual with perforate hibernation epiphragm. Stippled area is attached to the substrate *in situ*. B. View through first whorl behind aperture, showing layer of epiphragmal bubbles. Scale lines = 1 mm



portant during the long periods of unfavorable conditions experienced by temperate species during winter. Supercooling may be an important mechanism of freeze-resistance in hibernating land snails (Riddle, personal communication) and contact of ice crystals or debris with the supercooled tissue might induce nucleation and freezing.

The thickened winter epiphragm of *Pupoides albilabris*, together with the habit of attachment during dormancy, provides excellent mechanical protection for the animal during hibernation. The outer barrier is not complete, however, presumably because respiration requires the presence of a pore. The imperforate secondary layer of bubbles completes the closure of the aperture, and, protected by the outer epiphragm, can be thin enough to allow diffusion of respiratory gases.

It is interesting to note that other pupillid species examined (*Gastrocopta armifera*, *G. contracta*, *G. procera*) did not form a thick hibernation epiphragm. In these species the aperture is protected by large lamellae which are lacking in *Pupoides*. A layer of thin epiphragmal bubbles, like that in *Pupoides*, was found at and behind the lamellae.

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NOTES & NEWS

A Range Extension of *Anachis lilliana* Whitney, 1978

BY

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Anachis lilliana Whitney, 1978, had been named from material collected at Playa Alicia near San Felipe, Baja California Norte, Mexico, under rocks at low tide, March, 1976. Other material examined had come from Bahía Adair, Sonora, Mexico; Libertad, Sonora, Mexico; Topolobampo Bay, Sinaloa, Mexico; Mazatlán, Sinaloa, Mexico; and San Blas, Nayarit, Mexico. All were collected intertidally. In addition, there was one isolated specimen that had been dredged from 9.0 - 22.5 m, off Punta Quepos, Puntarenas Province, Costa Rica, 9°52' 43" N; 84°09'41" W.

As the above list indicates, there is a band of collecting stations extending from Bahía Adair just north of Puerto Peñasco to San Blas. The one potential station from which no specimens had been reported was Guaymas, Sonora, Mexico. As this area is rich in mollusks, it seemed probable that *Anachis lilliana* was present in this area, but unreported.

On January 8, 1978, my wife and I were collecting shells at Soldado Bay, an area just N of Guaymas. We overturned rocks and swept the adhering material into vials for later examination and identification. At home we noted numerous specimens of *Anachis pygmaea* (Sowerby, 1832), 2 *A. hilli* Pilsbry & Lowe, 1932, and one lone specimen of *A. lilliana*. We now can include Guaymas in the list of collecting stations and consequently assume that *A. lilliana* may be found intertidally along the west coast of Mexico from Bahía Adair, Sonora to San Blas, Nayarit.

Errata

The following corrections should be made in the article by Clifford M. Nelson in our October 1978 issue:

Figures 6 and 7 should be transposed (on the first plate).

On page 210, right column, line 13, delete: southern.

On page 214, under entry for Allison, 1977b, 3rd line, substitute P for p in the word "programs."

On page 215, entry for Salin, 1972, 4th line, replace Ust' Kamchatka with: Ust' Kamchatsk.

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A VERY GENEROUS DONATION to the Endowment Fund of the C. M. S., Inc. was received from the Conchological Club of Southern California, for which we express our thanks. We cannot stress enough how important such donations are for the continued existence of our journal, nor can we express how much they do encourage us in our continuing efforts to make the Veliger better and bigger, issue by issue. Again, many thanks to our Friends of the C. C. S. C.

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The Seventh International Malacological Congress will be held from 31 August to 6 September 1980 at Perpignan and Banyuls-sur-Mer in France. With the change from Unitas Malacologica Europaea to Unitas Malacologica, membership is now open to all scientists interested in all topics concerning mollusks.

Papers may be presented at the Congress in English, French or German; any topic about living or fossil mollusks will be welcome. The international malacological journal, Malacologia, will, as in the past, publish abstracts of the papers presented.

Dr. Jean M. Gaillard, of the Muséum Nationale d'Histoire Naturelle, 55 Rue de Buffon, F - 75005 Paris, is President, Dr. Oliver E. Paget, Naturhistorisches Museum Wien, Austria, is Secretary and Dr. Peter Jung, Naturhistorisches Museum Basel, Switzerland, is Treasurer.

Further information may be obtained from the Secretariat for the 1980 Congress, Laboratoire B. I. M. et Malacologie, 55 Rue de Buffon, F - 75005, Paris, France. For membership, applications may be sent to Dr. Paget, Naturhistorisches Museum, Burgring 7, A - 1014, Vienna, Austria.

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Supplement to Volume 14: \$6.-.

[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 16: \$8.-.

[The Panamic-Galapagan Epitoniidae by Mrs. Helen
DuShane]

Orders for any of the publications listed above should be
sent directly to Mr. Art West. If orders are sent to us, we
will forward them. This will necessarily result in delays.

A Glossary of A Thousand-and-One Terms
Used in Conchology

by WINIFRED H. ARNOLD

originally published as a supplement to volume 7 of the
Veliger has been reprinted and is now available from
The Shell Cabinet, Post Office Box 29, Falls Church,
Virginia 22046, U. S. A. The cost is US\$ 3.50 postpaid
if remittance is sent with the order.

Supplement to Volume 15: Our stock is exhausted, but
copies are still available from The Shell Cabinet, P. O.
Box 29, Falls Church, Virginia 22046.

[A systematic Revision of the Recent Cypraeid Family
Ovulidae by CRAWFORD NEILL CATE]

Other supplements:

[Growth Rates, Depth Preference and Ecological Succes-
sion of Some Sessile Marine Invertebrates in Monterey
Harbor by Dr. E. C. Haderlie]

Supplement to Volume 17: Our stock of this supplement
is exhausted. Copies may be obtained by applying to Dr.
E. C. Haderlie, U. S. Naval Post-Graduate School, Mon-
terey, CA (lifornia) 93940.

Supplement to volume 18: \$10.50 postage paid.

[The Biology of Chitons by Robin Burnett *et al.*].

(Our supply of this supplement is exhausted; however,
copies may be available by making application to the
Secretary, Hopkins Marine Station, Pacific Grove, Cali-
fornia 93950.)

WE ARE PLEASED to announce that an agreement has
been entered into by the California Malacozoological
Society, Inc. with Mr. Steven J. Long for the production
and sale of microfiche reproductions of all out-of-print
editions of the publications of the Society. The microfiches
are available as negative films (printed matter ap-
pearing white on black background), 105mm × 148mm
and can be supplied immediately. The following is a list
of items now ready:

Volume 1: \$1.50	Volume 6: \$4.50
Volume 2: \$3.00	Volume 7: \$6.00
Volume 3: \$3.00	Volume 8: \$6.00
Volume 4: \$4.50	Volume 10: \$9.00
Volume 5: \$4.50	Volume 11: \$9.00

Volume 12: \$9.00

Supplement to Volume 6: \$1.50; to Volume 18: \$3.00

California residents please add the appropriate amount for sales tax to the prices indicated.

Please, send your order, with check payable to Opisthobranch Newsletter, to Mr. Steven J. Long, 792 Laurie Avenue, Santa Clara, CA 95050.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA (lifornia) 93644. Orders should be sent directly to Mr. West.

Single Copies of "The Veliger":

We have on hand some individual copies of earlier issues of our journal and are preparing a list of the various issues available with the prices. Some issues are present in only one or two copies, while others may be present in 10 or more copies. As we are anxious to make room, we will offer these numbers at an exceptionally low price. This list will be presented in a forthcoming issue in the Notes and News section.

These individual issues will be available only directly from the Society. Details on how to order such copies will be given when the list is published.

Subscription rate for volume 22 in the U. S. A. is \$30.- plus \$1.50 for mailing costs; the rate for all foreign countries is Swiss Franks 60.- plus SF 7.- for mailing. Details have been sent to all our subscribers and subscription agents with whom we deal.

We must emphasize that under no condition can we accept subscription orders or membership applications for calendar year periods. If "split volumes" are required, we must charge the individual number costs. Individual issues sell at prices ranging from US\$12.00 to US\$30.00, depending on the cost to us.

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of the remittance. The same policy applies to new members.

THE VELIGER is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject

to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of \$1.- to a percentage of the value of the draft, going as high as 33%. Therefore we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of United California Bank in Berkeley, California. This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable except as indicated elsewhere in this section.

Publication Date of THE VELIGER

THE PUBLICATION DATE of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICBN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US\$8.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US\$18.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

Claims for defective or missing pages must reach us within 60 days from the publication date. We will not respond to claims of missing issues made less than 30 days by domestic addressees, or less than 60 days by foreign addressees after the publication date of our journal issues. This refusal is necessary as we have received an increasing number of "claims" as much as 6 months before the claimed issue was to be published. We wish to conserve our energy and the cost of postage and stationery for more productive purposes.

Supplements

Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

Requests to be placed on this special mailing list should be sent to Dr. George V. Shkurkin, *Manager*, 1332 Spruce Street, California 94709

However, until further notice, we are suspending the publication of supplements until it will be reasonably certain that we will not be forced to spend many hours in tracing of lost insured or registered parcels and entering claims for indemnification. The special mailing list of members and subscribers who have entered an "including all supplements" will be preserved because of our innate optimism that sometime within our lifetime the postal services throughout the world will return to the former excellent and reliable performance.

Moving?

If your address is changed it will be important to notify us of the new address at least **six weeks** before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. Effective January 8, 1968 the following charges must be made:

change of address - \$1.-

change of address and re-mailing of a returned issue

- \$2.75 minimum, but not more than actual cost to us.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

At present we are charged a minimum fee of \$12.50 on each order for new addressograph plates. For this reason we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

The regulations pertaining to second class mailing require "pre-sorting" of the mail which involves a large amount of time, especially if the total number of pieces is too small to warrant the employment of computerization. This requirement seems justified as long as the rates for second class matter remain substantially below those for first class matter. However, our members should be aware of the fact that postal regulations rule that second class matter can not be forwarded three months after an address change, even though the addressee guarantees forwarding postage (in contrast, first class mail, at least for the time being, is forwarded for one year and that without charge!). Thus, issues mailed to the "old" address will be returned to the publisher if return postage is guaranteed at a rate that is considerably higher; we have been charged as much as \$1.80 for such returned copies. There is also a charge of 25¢ for a postal notification of the new address. It must be obvious that we cannot keep absorbing such extra expenses and keep membership dues and subscription rate at the current low rate. We must ask for the wholehearted cooperation of all concerned to help us to hold the line against increases. Also, if a copy is returned we will, as in the past, advise the member of this fact and indicate the total costs incurred for which we must seek reimbursement. If this reimbursement is not made, we cannot continue to send future issues to the delinquent member. Membership will have to be

considered as terminated and can be re-instated only upon payment of all arrears. We regret that this apparently hard rule is necessary, but we wish to continue publishing the Veliger - which will not be possible if these rules are not observed.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of \$4.25 (to reimburse us for the expenses involved in redeeming them) and at \$.95 per \$1.- face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

CALIFORNIA

MALACOOLOGICAL SOCIETY, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, the VELIGER. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C. M. S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, devices are deductible for Federal estate and gift tax purposes under section 2055, 2106, and 2522 of the Code. The Treasurer of the C. M. S., Inc. will issue suitable receipts which may be used by Donors to substantiate their respective tax deductions.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15

but before March 15 of the following year, there will be a re-instatement fee of \$1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of \$5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is \$25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

REGARDING POSTAL SERVICE

Complaints regarding late arrival of our journal are increasing in number, steadily, continually. However, we very conscientiously dispatch our journal on the printed publication dates. What happens after deposition at the Post Office is, of course, beyond our control. From some of our members we have been able to construct a sort of probable delivery schedule. In general, within California, 8 days is usual; outside of California, the time lapse increases with the distance; the East Coast can consider a lapse of "only" two weeks as rapid service; 4 to 5 weeks are not uncommon. Foreign countries may count on a minimum of one month, six weeks being the more usual time requirement and over two months not rare!

The Latest New Postage Rates

Effective on May 29, 1978, the U. S. Postal Service increased rates for first, third and fourth class matter, as announced some months before. However, although not announced publicly and without notification to publishers, second class postage rates within the United States were

also increased. Further, again without advance notification, postage for second class matter to the so-called PU-AS countries (Spanish-speaking countries and Brasil), which had traditionally been lower than to all other foreign countries, was increased to the same rate.

On July 6 a further increase of postage rates within the United States went into effect. This increase came also as a surprise to us, since we had assumed that the May increase was taking the place of the so-called phased increases which are scheduled for the sixth of July each year.

It is obvious that we are forced to pass these increases on to our members and subscribers. Therefore, effective immediately, we must charge US\$3.50 for postage to all addresses outside the United States, and \$1.50 for all domestic addresses.

Under no circumstances are we able to supply free replacement copies of issues that fail to reach their proper destination. However, we will ship by insured mail replacement copies at half the announced single copy rate of the particular issue plus postage. We have developed a triple check system so that, if we say that a copy has been mailed, we are absolutely certain that we delivered that copy to the post office in Berkeley and on the date we indicate. From our experience with the loss of insured mail, we are tempted to suggest that subscribers figure on a 10% reserve fund for the purchase of replacement copies. The only alternative remaining would be for us to increase subscription rates and membership dues by at least 10%. This, however, does not seem quite fair to us as some of our subscribers in almost 20 years have never failed to receive their copies.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion

that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time, that is 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed \$200.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, \$200.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U.S.A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are submitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript – including figure explanations and the "Literature Cited" section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the "dead letter" office, in other words, it is destroyed.

BOOKS, PERIODICALS, PAMPHLETS

Proceedings of the First International Congress on Pacific Neogene Stratigraphy, Tokyo, 1976

Edited by TSUNEMASA SAITO and HIROSHI UJIE, Science Council of Japan and Geological Society of Japan, 433 pp. July, 1977. \$40.00 from Kaiyo Shuppan Co., Ltd., 7-5 Sanban-cho, Chiyoda-ku, Tokyo 102, Japan (% Dr. Hiroshi Ujiiie).

This volume summarizes the status of Neogene stratigraphic paleontology of the Pacific Ocean Basin with respect to borehole data from the Deep Sea Drilling Project (DSDP) and data from land-based sections around the Pacific rim. The North Pacific is emphasized. Contents represent a thorough recapitulation of the initial congress proceedings of the Regional Committee on Pacific Neogene Stratigraphy (RCPNS) held in Tokyo during May 1976; the RCPNS consists of earth scientists, primarily stratigraphic paleontologists (biostratigraphers), studying the late Cenozoic of the Pacific Ocean Basin.

Sixteen papers which were presented during the General Sessions deal with broad aspects of Pacific Basin stratigraphy and paleontology. Although the emphasis is on microfossils, especially planktonic foraminifers, three papers deal with molluscan biochronologies. GLADENKOV considers the stages of evolution of late Cenozoic molluscan faunas in the boreal North Pacific; he includes an updated definition and faunal characterization of marine molluscan horizons (stages) in the eastern U. S. S. R. and points out certain correlations with the Neogene of Japan and the eastern North Pacific. SHUTO reviews the molluscan chronology of southeastern Asia, correlating such widely separated sections as Pakistan, Java, and the Philippines with the western North Pacific molluscan sequence in Japan. A review by ADDICOTT of middle to late Tertiary molluscan sequences in the eastern North Pacific margin (California to Alaska) and also of the paleogeography of marine basins of deposition is included.

Extended abstracts of 53 papers delivered at sectional meetings during the congress are published in the later part of this volume. Of special interest to molluscan specialists are useful resums of 11 papers on «Mollusca and Other Mega-Invertebrates». Papers include syntheses of the late Tertiary molluscan biostratigraphy of Alaska (ALLISON) and of the Japanese Islands (CHINZEI); the former deals primarily with the age and correlation of sections along the Pacific coast of Alaska, the latter with

the climatic and paleogeographic history of the Japanese Islands. Other papers treat faunal migration (KILMER, KANNO), turritellid phylogeny (KOTAKA), nepitunoid phylogeny and zoogeography (NELSON), pectinids of the North Pacific (MASUDA), biostratigraphy of the southern part of the Korean Peninsula (YOON), correlation of Atlantic and Pacific high-latitude sequences (GLADENKOV), and interrelation of the molluscan and planktonic foraminiferal sequences in Japan (TSUCHI and IBARAKI).

This proceedings volume of the congress ranks as a valuable and timely summation of the various chronologic schemes (microfossil, molluscan, radiometric, and magnetostratigraphic) that are being effectively utilized in correlation of the Neogene of the Pacific Ocean Basin.

W. O. Addicott

Catalogue of Molluscan Taxa

Described by Tadashige Habe During 1939 - 1975, with Illustrations of Hitherto Unfigured Species

by TÔRU INABA and KATURO OYAMA. Okinaebishu-nokai, 4-18-7 Tsukushiga-oka, Kashiwa City, Chiba Pref., Japan. iv + 185 pp., 7 pls. & portrait. Price not stated.

December 1977

This handsome softcovered volume, compiled in commemoration of Dr. Habe's 60th birthday, contains entries for 1089 generic and specific names proposed in 265 taxonomic papers from the pen of this prolific malacologist between 1939 and 1975. In addition to name (and authorship where shared by Habe and another) and citation of the original description, each entry includes (for genera) type-species - with original reference - and method of fixation, or (for species) type locality and collector, measurements and museum numbers of type material. Other significant literature citations, such as illustrations of type material, are included, as are notes on family placement, a few emendations of type locality, notes on homonymy and synonymy, and etymology of latinized Japanese names. This portion of the work is in English. Also within these covers are a dedicatory address by Iwao Taki (in Japanese), portrait of Dr. Habe and capsule biography (in Japanese), explanation of format (bilingual), lists of co-authors and persons to whom taxa were dedicated (principally in Japanese), list of molluscan taxa dedicated to Dr. Habe, index map of frequently cited western Pacific localities (in English), bibliography of Dr. Habe's taxonomic papers up to 1975 (bilingual), and 7 plates of illustrations, many of them hitherto unfigured type specimens. Quality of the photographs is, in

general, good, most of them grouped on a black background.

Dr. Habe's output naturally invites comparison with that of other prolific describers of taxa, and while far short of Dall's (5427) or Pilsbry's (5680) catalogued taxa (Boss, ROSEWATER & RUHOFF, 1968, U. S. Nat. Mus. Bull. 287: 4), comes surprisingly close to A. A. Gould's 1088 species and genera (JOHNSON, 1964, U. S. Nat. Mus. Bull. 239: 32). Dr. Habe's work, of course, continues to the present.

This book is certain to prove a valuable reference volume and to increase access to a significant descriptive literature. The annotations concerning synonymy and subsequent critical treatments of Habean taxa are not only useful but must have greatly increased the time and effort required to put together this work. In producing such a thorough and elaborately realized catalogue, the compilers honor themselves as well as Dr. Habe.

B. Roth

Malacological Review

P. O. Box 420, Whitmore Lake, Michigan 48189, U. S. A.
vol. 11 (1-2), viii + 212 pp.; illust. 1978

We have had the pleasure of reviewing this annual publication since its inception and we have always been impressed by its enormous value to the active worker in malacology. We are at a loss to say what we have to say in a new way. So we will not even try, except, perhaps, to state that this latest volume is as excellent as its predecessors. It has the same arrangement of material. Two review articles, followed by two research articles and two brief communications, 82 abstracts of papers presented at the 5th Meeting on the Investigation of Molluscs, Leningrad, 1975; and the list of articles in the current periodical literature from all countries.

That inflation is affecting this publication as well as all others is not surprising. What is surprising, however, is how little the cost increases are reflected in the new subscription rates: vol. 12 will be \$17.- for institutions and \$10.- for individuals in the U. S. A., \$10.50 for private subscribers in any other country.

R. Stohler

1978 - 1979 International Directory of Conchologists

published by the Shell Cabinet, P.O. Box 29, Falls Church, Virginia 22046, U. S. A. 47 pp. \$3.50 (incl. postage).

The 3rd edition of this well-organized list of shell collectors and malacologists will be welcome by all actively

engaged in exchanging shells on a world-wide basis. It will also be useful to scientific workers who may need to obtain research material from sometimes difficult to reach localities. This particular aspect is facilitated by the arrangement of names in alphabetical order under geographical headings, as well as by the indication behind each name (and address) of the special interest of the person listed.

R. Stohler

Field Guide to Seashells of the World

by GERT LINDNER; translated and edited by GWYNNE VEVERS. 271 pp. of which ca. 130 are color pls.; and many b&w illustr. Van Nostrand Reinhold Company. New York. Soft cover, \$8.95.

In spite of an apparent overabundance of shell books, the present volume stands out among its competitors because of the thoroughness of the general part on the various molluscan families and the careful treatment of the selected samples of the various taxa. In contrast to many other similar books, the author here does not «invent» common names; thus, where common names are given, one may feel assured that these are indeed in use, at least in some areas where the particular species are common.

We think that this book will be very useful even to him who has all the other shell books of a similar nature.

R. Stohler

Polymorphism in Marine Mollusks and Biome Development

by ARTHUR H. CLARKE. Smithsonian Contributions to Zoology, No. 274. 14 pp.; 5 figs. in text 1978

We are quoting an important paragraph from this paper which, in our opinion, tells best what the entire paper demonstrates:

"One of the major points of this paper is that the nature and intensity of natural selection appears to be significantly different within communities of shallow-water arctic, shallow temperate, shallow tropical, and deep-sea marine mollusks. It therefore provides a caveat against attempts to apply in one biome a hypothesis concerning natural selection or an ecological "principal" [sic] that was originally proposed to explain phenomena observed in a different biome."

R. Stohler

**A Catalog of the Type-Specimens
of Recent Cephalopoda in the National Museum
of Natural History**

by CLYDE F. E. ROPER and MICHAEL J. SWEENEY. Smithsonian Contributions to Zoology, No. 278. 19 pp.
16 August 1978

This is a well organized list of cephalopod types (holo- and paratypes) in the collection of the National Museum of Natural History. It will, like similar lists of types in the same and in other public collections be of great value in stabilizing nomenclature if – and that is, of course, the ever recurring “if” – the list is used properly by the appropriate researchers. By “using the list,” we mean: using it to get the material needed for comparison in order to avoid a “stillborn” name, a junior synonym.

R. Stohler

of Sea and Shore

This popular quarterly publication continues to bring articles of various calibers, something for the taste of everyone. However, in recent issues the editor, Tom Rice, has started to reprint taxonomic papers that have been published previously. While in itself this may be very useful in bringing less accessible works to the attention of the active shell collectors, we are disturbed by the fact that taxa described as new in the original publication are also designated as “spec. nov.” or its equivalent. This is most unfortunate as it can lead the unwary or especially the novice to an erroneous designation of his specimens by adding the year of the second publication to his shell’s name instead of the date of the actual original description. The only correct way is to list the actual year of the first naming of a taxon in the reprinting and omitting the designation “spec. nov.” Aside from this flaw, we continue to enjoy each issue and are amazed at the variety of advertisements offering shells from every corner of the world.

R. Stohler

The following papers deal with Ammonites. They are all published in 1977 in “Stuttgarter Beiträge zur Naturkunde,” published by the Staatliches Museum für Naturkunde in Stuttgart, Series B, Geology and Paleontology.

To conserve space, the bibliographic citations will be abbreviated to “SBN (B), Nr.” followed by the number and pagination and illustrations.

**Über das Vorkommen von *Tmaegoceras* Hyatt
(Ammonoidea) im Lias Europas**

by GUNTER GEBHARD and RUDOLF SCHLATTER. SBN (B) No. 22: 15 pp.; 1 plt.; 3 text figs. 30 May 1977

The Lower Jurassic in Southwestern Germany

by MAX URLICHS, SBN (B) No. 24: 41 pp.; 6 pls.; 11 text figs.; 2 tables 1 September 1977

The Braunjura (Brown Jurassic) in Southwest Germany

by GERD DIETL. SBN (B) No. 25: 41 pp.; 7 pls.; 14 text figs.; 1 table 15 July 1977

The “White” (Upper) Jurassic in Southern Germany

by BERNHARD ZIEGLER. SBN (B) No. 26: 79 pp.; 11 pls.; 42 text figs. 30 June 1977

**Stratigraphy, Ammonite Fauna and some Ostracods
of the Upper Pliensbachian at the Type Locality
(Lias, SW-Germany)**

by MAX ULRICHS. SBN (B) No. 28: 13 pp.; 2 pls.; 2 text figs. 1 July 1977

The Aalenian at the Type Locality

by GERD DIETL and ANDREAS ETZOLD. SBN (B) No. 30: 13 pp.; 2 pls.; 3 text figs. 15 May 1977

***Hybopeltoceras*, ein neuer Hybonoticeratide
(Ammonoidea) aus dem oberen Jura der Betischen
Kordilleren (Subbetischer Zone), Andalusien,
Südspanien**

by FEDERICO OLORIZ. SBN (B) No. 32: 9 pp.; 1 plt.; 4 text figs. 1 September 1977
R. Stohler

After the October issue had been mailed, we discovered a disturbing error in the sequence of figures and in the figure explanations of the article by Dra. Marta Bretos. We present here, with our apologies to our members and subscribers, but especially to Dra. Bretos, corrected substitute pages. It was, however, not possible to place the figures in the correct sequence, but the correct numbers and explanations are with the corresponding figures; also, the correct Figure 5 is in place of the erroneously printed figure.

The Editor

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

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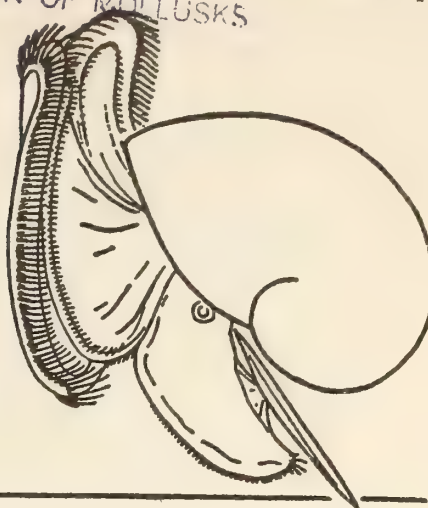
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Ultrastructure of the Mosaicostracal Layer in the Shell of the Bivalve *Mytilus edulis*

BY

MELBOURNE R. CARRIKER

College of Marine Studies, University of Delaware, Lewes, Delaware 19958

(2 Plates)

INTRODUCTION

THE MOSAICOSTRACUM, a thin discrete calcareous layer continuous over the outer surface of the valves between the periostracum and the outermost shell layer of bivalves, was discovered by HAMILTON (1969; see also GRÉGOIRE, 1972). Using replicas and the transmission electron microscope, Hamilton described the layer in the valves of several species of the family Tellinidae. He concluded that in this family the mosaicostracum displays patterns which are easily recognized, are definitive for each species examined, and appear to be taxonomically consistent at the species level.

In the course of an experimental ultrastructural study of dissolution of the shell of *Mytilus edulis* Linnaeus, 1758 by various synthetic chemicals and the secretion of the accessory boring organ of the gastropod *Urosalpinx cinerea* (Say, 1822) (CARRIKER, 1978), I had the opportunity to examine the mosaicostracum in *M. edulis*. The layer has not been described in this bivalve before. The purpose of this paper is thus to illustrate the mosaicostracum of *M. edulis* and to describe the fine structural relationship between the mosaicostracum, the periostracum, and the prismatic region of this bivalve.

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Thanks are expressed to Virginia Peters for collaborating in the scanning electron microscopy (JOEL JSM-U3, Woods Hole Oceanographic Institution), and to Walter S. Kay for preparing the final prints for publication. The research was begun during my tenure in the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, and completed at the University of Delaware. It was supported in part by Public Health Service Research Grant DE 01870 from the National Institute of Dental

Research. University of Delaware, College of Marine Studies Contribution Number 117.

MATERIALS AND METHODS

Rapidly growing specimens of *Mytilus edulis*, approximately 5 cm long, were collected in the vicinity of Woods Hole. Valves, freshly cleaned of soft tissues and washed in tap water, were shattered on towelling with a blow from a hammer. Pieces of shell, approximately 2 to 5 mm in longest dimension, were selected under the binocular microscope from the thick middle region of valves. These pieces were treated as follows:

a) Several fragments of shell were immersed in 20 mL of undiluted hydrogen peroxide (H_2O_2 , 31.8%, Baker analyzed reagent) in small beakers. Beakers were covered with a watch glass and placed close to a black light (Spectrolite, 115 v, 60 cycle, with two 17 inch [ca. 42.5 cm] tubes; see SWIFT, 1966), and left in that position for 7.5 hours. Temperature of the medium rose from about 20 to 27°C during exposure to the ultraviolet radiation. Specimens were then rinsed in tap water, dried with a stream of warm air, mounted on scanning electron microscopy stubs with fast drying epoxy, desiccated in an oven at 60°C for 2 days, and examined with the scanning electron microscope.

b) Fragments of shell, prepared as in a), were immersed in small beakers in 150 mL of sodium hypochlorite (5.25%, commercial clorox). One set was left in clorox for 10 minutes and sonicated (ultrasonicator, 75 kc, 55 watts) for 5 minutes, another in clorox for 18 minutes and sonicated for 12 minutes, and a third in clorox for 2.75 hours and sonicated for 65 minutes at approximately 12 minute intervals.

The mosaicostracum was examined ultrastructurally in a total of 6 different sets of shell fragments from different individuals of *Mytilus edulis*. In addition, the

layer was observed at the edge of boreholes excavated in valves of *M. edulis* by *Urosalpinx cinerea* at the rim where the periostracum peeled back from the mosaicostracum during drying, revealing the matching surfaces of mosaicostracum and the periostracum (CARRIKER, 1978).

OBSERVATIONS

The mosaicostracum of *Mytilus edulis* was exposed for examination by 3 separate treatments: a) thinning of the periostracum by surficial dissolution with hydrogen peroxide and ultraviolet radiation, resulting in the cracking and peeling of the remaining periostracum in spots as it dried; b) thinning of the periostracum by solubilization by the secretion of the accessory boring organ of *Urosalpinx cinerea* at the rim of the boreholes, resulting in the peeling back of the periostracum from the edge of the borehole during drying; and c) dissolution of the periostracum with clorox followed by sonication. In treatments a) and b) separation of the periostracum from the mosaicostracum was complete in many places, leaving no mosaicostracal crystals on the underside of the periostracum (Figures 1, 3, 6, 12). Treatment of shell fragments with clorox and sonication cleanly dissolved most of the periostracum in 18 minutes, whereas prolonged treatment, although it removed all of the organic layer, caused erosion and smoothing of the top surfaces of the largest tubercles (compare Figures 5, 7, 9, 10); however, the general configuration of the tubercles was not altered. Application of clorox without sonication, even for periods as long as 40 hours, solubilized only portions of the periostracum (Figure 8), and explains why HAMILTON (1969) was forced to treat his valves with clorox for

periods as long as 30 to 60 days. Peeling of the periostracum permitted matching of surfaces of mosaicostracum and periostracum (see Figures 1, 3-4, 11-12), and exposed surfaces that were unaffected by solvents and thus served as controls for the appearance of normal mosaicostracum.

Ultrastructural examination of matching surfaces of mosaicostracum and periostracum (Figures 3-4, 5-6, 11-12) demonstrated the closeness of fit of the 2 layers in the intact position. The height of tubercles, and corresponding depressions in the periostracum, ranged from a fraction of a micrometer to about $7\mu\text{m}$, and was highly variable (Figures 7, 9, 11). In some places mosaicostracal tubercles occurred in distinct rows (Figure 7), and in others, distribution seemed random (Figures 9, 11). Under peels resulting from thinning of the periostracum with hydrogen peroxide and ultraviolet radiation (Figures 4, 5) where no dissolution of the mosaicostracal crystals occurred, the minute sharply angled projections of tubercular surfaces were clearly evident. The smallest projections measured $0.1\mu\text{m}$ in thickness. Alignment of rows of tubercles in some instances seemed associated with growth bands in the underlying prismatic layer of shell (Figure 1). Figures 8 and 9 suggest that a thin veneer of mosaicostracal crystals was deposited over the prismatic layer, serving as a supporting layer for the tubercles.

DISCUSSION AND CONCLUSIONS

The finely convoluted exterior surface of the mosaicostracum and matching depressions on the underside of the periostracum of *Mytilus edulis* strongly suggest that the principal function of the mosaicostracum is to bond the periostracum and the prismatic strata of the shell together.

Explanation of Figures 1 to 6

Figure 1: Underside of periostracum, thinned by treatment with hydrogen peroxide and ultraviolet radiation for 7.5 hours, periostracum peeled back during drying to expose mosaicostracum. Patch of bare periostracum (p), and corresponding patch of intact mosaicostracum (m): prismatic stratum (pr). Scanning electron micrograph.

Scale bar = $125\mu\text{m}$

Figure 2: Edge of part of mosaicostracum clinging to underside of periostracum; mosaicostracal crystals at left (m), and underside of periostracum at right (p) (magnified part of Figure 1). Scanning electron micrograph.

Scale bar = $5\mu\text{m}$

Figure 3: Enlarged view of underside of periostracum taken in bare patch in Figure 1, illustrating the range of variation of the depressions and projections of the surface. Scanning electron micrograph.

Scale bar = $10\mu\text{m}$

Figure 4: Enlarged view of part of surface of mosaicostracum fitting into periostracum shown in Figure 3 before layers were separated. Pattern of tubules corresponds with that in the periostracum. Scanning electron micrograph.

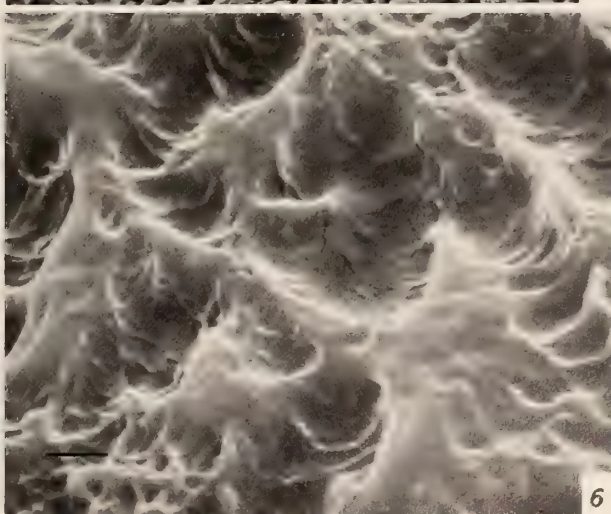
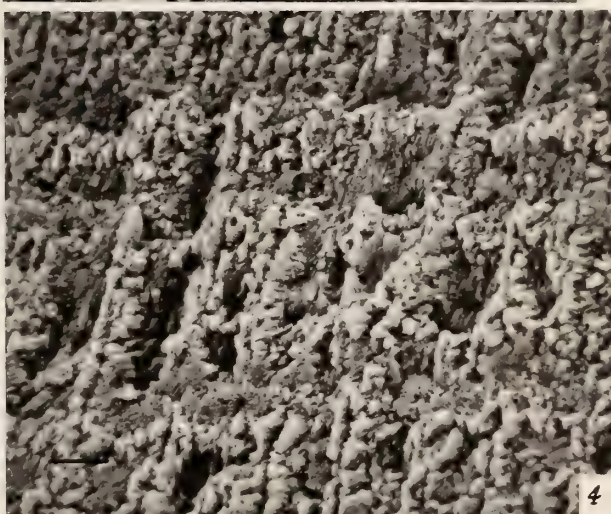
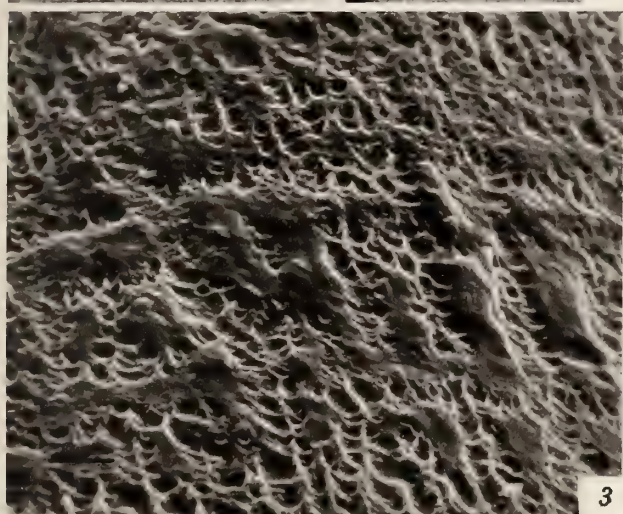
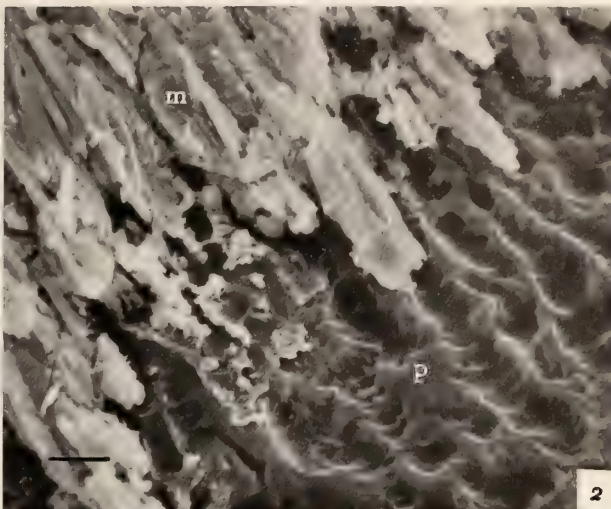
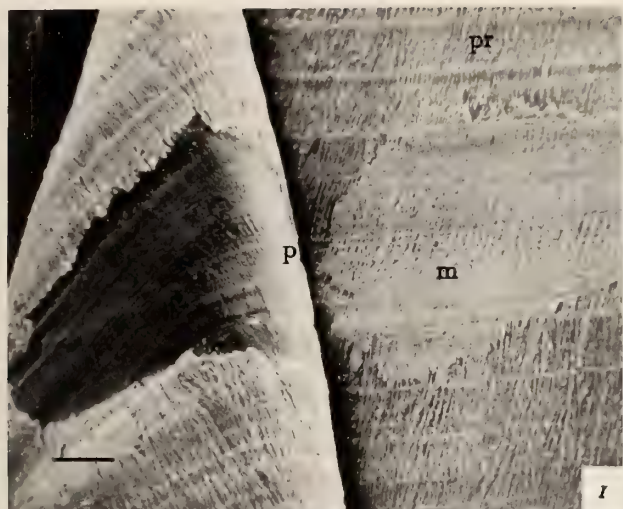
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Figure 5: Enlarged view of upper surface of mosaicostracum from which periostracum peeled away during drying, taken in area designated by m in Figure 1. Illustrates highly tubercular surface covered with minute sharp projections. Scanning electron micrograph.

Scale bar = $1.7\mu\text{m}$

Figure 6: Enlarged view of under surface of periostracum in vicinity of area from which it peeled away from mosaicostracum in Figure 5. Scanning electron micrograph.

Scale bar = $1.7\mu\text{m}$





That integration of these layers is admirably served is attested by the firmness with which the periostracum coheres to the shell. The height and prominence of major tubercles, and the depth to which they penetrate the periostracum, is probably a function of the relatively thick periostracum. By contrast, HAMILTON (1969) reported that the mosaicostracum in individuals in the family Tellinidae is relatively thin, only about $0.3\mu\text{m}$ thick; this may be the result of the thin periostracal layer usually encountered in these species. The configuration and height of tubercles in *M. edulis* probably not only effectively cement the periostracum to the prismatic layer, but also prevent the periostracum from sliding over the shell when pressure is applied. This feature is an advantage to an organism that, in close juxtaposition to its neighbors, often lives exposed intertidally to the pounding of waves.

Apparently the bond between mosaicostracal and prismatic layers, both mineralized strata, is adequate for adhesion without additional substructures. When long axes of prisms are positioned at approximately right angles to the surface of the mosaicostracum, interstices among prism ends apparently provide ample crevices for adhesion of the mosaicostracum. Prisms lying nearly parallel to the surface (as in Figure 8) also appear to afford sufficient variation in contour to provide a firm grip for the mosaicostracum.

HAMILTON (1969) tentatively grouped and named the patterns of the external surface of the mosaicostracum in the Tellinidae in 5 major categories. None of these patterns characteristic of the Tellinidae corresponded with that of *Mytilus edulis*. This is not unexpected as the families Tellinidae and Mytilidae are not close taxonomically. The name "tuberculate" is suggested here for the mosaicostracal pattern in *M. edulis*.

D'ATTILIO & RADWIN (1971) named a thin layer on the surface of the valve of several species of 4 families of gastropods, the intritacalx. They noted that in many cases this layer was characterized by an intricate sculpture which did not always correspond to that of the underlying shell, and in many individuals the layer was found underneath a thin periostracum. It appears that D'Attilio & Radwin's intritacalx is homologous to Hamilton's mosaicostracum. Since the term mosaicostracum was the first proposed, it is used in this paper. None of the intritacalxal patterns described by D'Attilio & Radwin correspond to the mosaicostracal pattern described here for *Mytilus edulis*.

Scanning electron micrographs of the mosaicostracum of *Mytilus edulis* do not reveal the internal structure of the

tubercles or of the basement layer. Study of the organic framework and surfaces of the mosaicostracum in contact with the periostracum and the prismatic zone could be undertaken by cleaving the nacreous stratum from the valves of young mytilids, demineralizing the prismatic-mosaicostracal-periostracal layers, and examining ultrathin sections of them with the transmission electron microscope. In *M. edulis* the nacreous layer is aragonitic and the prismatic zone is calcitic. In the oyster, *Crassostrea virginica* (Gmelin, 1791), larval valves and myostracal muscular attachment sites are aragonitic (STENZEL, 1964). In view of the fact that the mosaicostracum in *M. edulis* serves as an attachment layer for the periostracum, it is possible this layer is also aragonitic. The matter needs investigation.

The fact that sonication greatly accelerates dissolution of periostracum when immersed in sodium hypochlorite will provide a useful technique for the comparative study of the mosaicostracum in other groups of mollusks. It is uncertain whether the mosaicostracum is unique to the phylum Mollusca, or whether the layer occurs in other shelled invertebrate groups, such as the Brachiopoda, where a protective outer covering is present. A comparative search for the layer in other shelled invertebrates will also be facilitated by the combined use of clorox and sonication.

SUMMARY

The fine structure of the mosaicostracum, a thin discrete calcareous layer continuous over the outer surface of the valves between the periostracum and the outermost shell layer of bivalves is described for the first time in the bivalve *Mytilus edulis*. The layer was exposed for ultrastructural examination by treatment with hydrogen peroxide and ultraviolet radiation, sodium hypochlorite and sonication, and secretion from the accessory boring organ of the gastropod *Urosalpinx cinerea*. The exterior surface of the mosaicostracum consists of a finely convoluted tubercular pattern with matching depressions on the underside of the periostracum. Height of tubercles and corresponding depressions in the periostracum range from a fraction of a micrometer to $7\mu\text{m}$. A thin veneer of mosaicostracal crystals is deposited over the prismatic layer, appearing to serve as a supporting layer for the tubercles. The configuration and height of tubercles effectively cement the periostracum to the prismatic layer, and prevent the periostracum from sliding over the shell when environmental pressures are applied.

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Explanation of Figures 7 to 12

Figure 7: Enlarged view of portion of exterior surface of mosaicostracum of *Mytilus edulis* exposed by treatment with clorox for 18 minutes and sonication for 12 minutes (which dissolved the periostracum), illustrating highly irregular tubercular shapes of crystals. Combined clorox and sonication treatment smooth tops of major tubercles slightly (compare with Figure 5). Scanning electron micrograph.

Scale bar = 5 μ m

Figure 8: Exterior surface of mosaicostracum treated only with clorox for 40 hours. Tubercles of mosaicostracum (m) affixed to prismatic layer (pr). Treatment did not dissolve all of periostracum (p) and remnants of it are visible at upper left. Scanning electron micrograph.

Scale bar = 1.7 μ m

Figure 9: Oblique view of fracture section of shell from which periostracum was removed by immersion in clorox for 10 minutes and sonication for 5 minutes, dissolving all periostracum. Prisms of prismatic region visible in fracture surface (pr), next left is smooth surface of fractured mosaicostracal crystals (mf), and to left of

this is tubercular surface of mosaicostracum (m). Scanning electron micrograph.

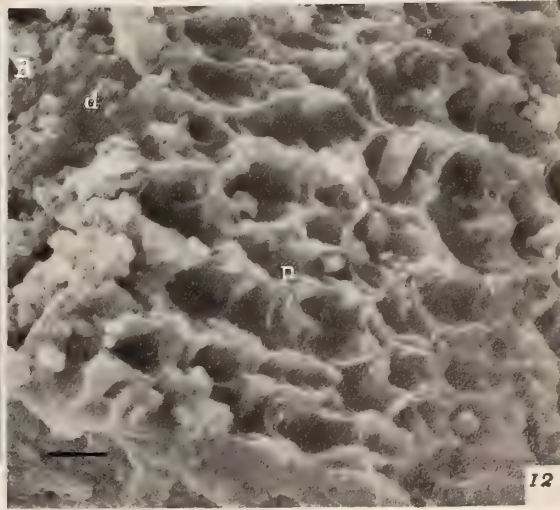
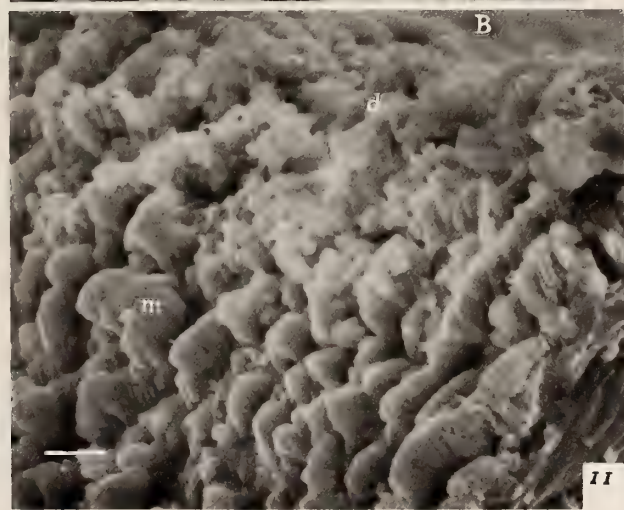
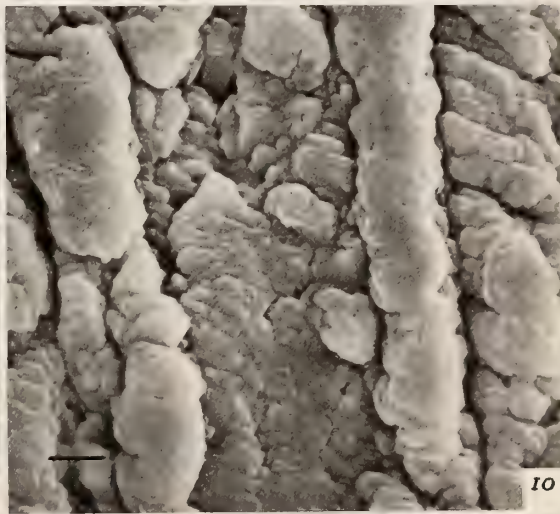
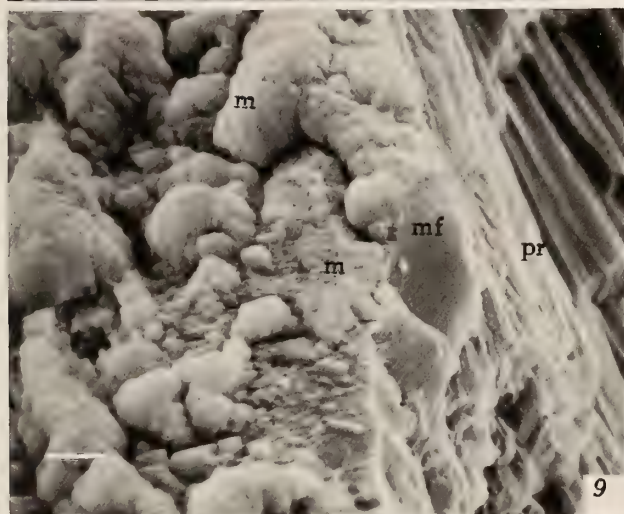
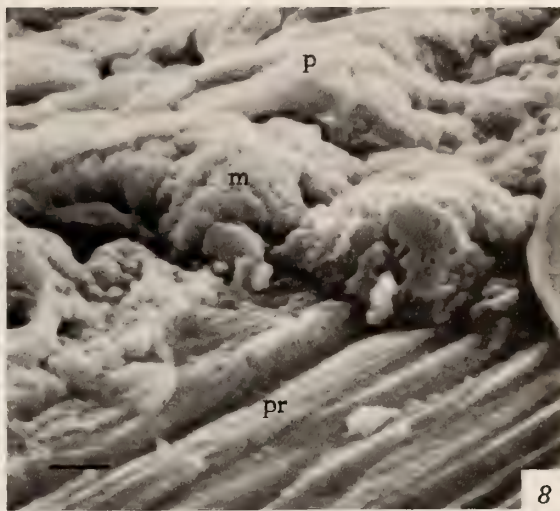
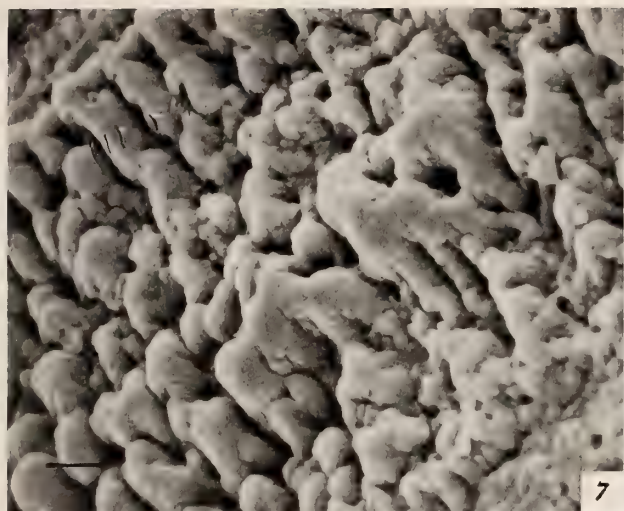
Scale bar = 2.5 μ m

Figure 10: Exterior surface of mosaicostracum after shell fragment treated with clorox for 2.75 hours and sonicated for 65 minutes to remove periostracum, showing rows of major tubercles and successively smaller tubercles between the major rows. Exposed tops of tubercles were smoothed of sharp projections by treatment (compare Figures 5, 7, 9). Scanning electron micrograph.

Scale bar = 2 μ m

Figures 11-12: Edge of bore hole (B) excavated by the gastropod *Urosalpinx cinerea follyensis* Baker, 1951 in shell of *Mytilus edulis* at spot where periostracum peeled back from mosaicostracum during drying. Figure 11. Intact mosaicostracal tubercles (m) at left and tubercles partly dissolved by secretion of accessory boring organ of *U. cinerea* at right (d). Figure 12: Normal undersurface of periostracum (p) at right and periostracum partially dissolved by secretion at left (d). Scanning electron micrograph.

Scale bar = 5 μ m





The Digestive Diverticula of *Alderia modesta* and *Elysia chlorotica*¹

(Opisthobranchia : Sacoglossa)

BY

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(3 Plates; 5 Text figures)

INTRODUCTION

THE MAJORITY OF ADULT sacoglossans are green in colour and a number of authors (KAWAGUTI & YAMASU, 1965; TAYLOR, 1968; TRENCH *et al.*, 1969) have shown that this coloration is attributable to ingested chloroplasts. Long-term associations between active algal chloroplasts and the digestive cells of sacoglossans appear to be restricted to the siphonaceous algae (Order Siphonales) and the elysiid sacoglossans (TRENCH, 1975). The eolidiform (cerata-bearing) sacoglossans, on the other hand, apparently retain chloroplasts for shorter time periods, often of less than 24 hours (HINDE & SMITH, 1974; McLEAN, 1976).

Elysia chlorotica (Gould, 1870) has not been examined for intracellularly functional chloroplasts but other species of the genus *Elysia* do retain functional chloroplasts (TAYLOR, 1968; TRENCH *et al.*, 1969; GREENE, 1970; and TRENCH *et al.*, 1973). *Alderia modesta* (Lovén, 1844) has been reported not to retain functional chloroplasts (HINDE & SMITH, 1974). In Nova Scotia the alga consumed by both *E. chlorotica* and *A. modesta* is an undetermined species of *Vaucheria* which forms fuzzy mats upon the salt marsh in summer and in winter occurs as a filamentous aquatic form in the numerous marsh pools. Both slugs occur in both habitats (BAILEY & BLEAKNEY, 1967; BLEAKNEY & BAILEY, 1967). As *Vaucheria* chloroplasts (Order Xanthophyta) have never been reported as establishing symbiotic associations with sacoglossans, the local situation provides an opportunity for a comparative morphological and functional study of two sympatric elysiid and eolidiform sacoglossans feeding on the same algal species. The situation is comparable to European investigations of the elysiid *E. viridis* (Montagu, 1804) and the eolidiform *Placida dendritica* (Alder & Hancock, 1843) feeding on the siphon-

aceous alga *Codium* (TRENCH, 1975; McLEAN, 1976). Thus, the purpose of this paper is twofold: (1) to provide a description and comparison of the structure of the digestive diverticula of *Alderia modesta* and *Elysia chlorotica* using light and electron microscope techniques, and (2) to assess the photosynthetic capabilities of chloroplasts of *Vaucheria* in *E. chlorotica* and *A. modesta* by studying light-mediated oxygen production.

MATERIALS AND METHODS

Specimens of *Alderia modesta* and *Elysia chlorotica* were collected from salt marshes of the Minas Basin, King's County, Nova Scotia. They were found in trenches and pools dominated by algae of the Cladophorales and on *Vaucheria* sp. mats in damp depressions at the base of *Spartina alterniflora*. Specimens were maintained in refrigerated jars of sea water or in an aerated salt water aquarium.

For histological study, tissues were fixed in Zenker's fixative, paraffin embedded and sectioned at 7 μ m. The sections were stained with either Ehrlich's hematoxylin and alcoholic eosin Y (THOMPSON, 1966) or with Mallory's trichrome sequence (LILLIE, 1965).

Several histochemical tests were used. Glycogen was demonstrated in Rossman's fixed, paraffin embedded tissues with the periodic acid Schiff's reaction (PAS) of Hotchkiss as described in THOMPSON (1966). Companion sections were digested with diastase to distinguish the glycogen from other PAS-positive substances. Ribonucleic acid (RNA) was demonstrated in Carnoy's fixed tissues with the methyl green-pyronin Y method of Brachet. To confirm the identification of RNA, control sections were digested with bovine ribonuclease for 2½ h before staining. Lipids were visualized in tissues fixed in either 10% formalin or in Baker's formol calcium, gelatin embedded, and sectioned at 10 μ m on a freezing microtome at -20°C.

¹ Supported by the National Research Council of Canada

Two neutral lipid methods were used, the oil red O method of Lillie and the propylene glycol-Sudan method of Chiffelle & Putt. Acid mucopolysaccharides were investigated in Zenker's fixed and paraffin embedded tissues. The Alcian blue method, staining at pH 2.5 for 30 min., as described by HUMASON (1972) was used. The Gomori method (HUMASON, *op. cit.*) was used to demonstrate acid phosphatase. Tissues were fixed in Baker's formal calcium, gelatin embedded, and sectioned on a freezing microtome at -20°C . An incubation time of 4 h at 37°C was used. Control sections were incubated in a substrate medium containing sodium fluoride to inhibit enzyme activity. Gomori's calcium-cobalt method was used to demonstrate alkaline phosphatase activity. The tissues were fixed in 80% ethanol at 4°C and paraffin embedded. An incubation time of 4 h at 37°C was used. Control sections were prepared in an identical manner except that the sodium glycerophosphatase was omitted from the incubation medium. Calcium was demonstrated in Carnoy's fixed, paraffin embedded tissues with the alizarin red S method of Dahl. Unless other references are given, the above techniques were applied as described by PEARSE (1961).

For electron microscope studies, tissues were fixed in 2.5% glutaraldehyde in filtered sea water, post-fixed in 1% osmium tetroxide in filtered sea water, and embedded in Durcupan. For orientation, thick sections were stained with 1% aqueous toluidine blue - 1% aqueous borax solution. The thin observational sections were stained with uranyl acetate and Reynold's lead citrate (PEASE, 1964) and studied with a Zeiss EM9S electron microscope.

Oxygen production was used as a criterion to measure photosynthetic activity in *Elysia chlorotica* and *Alderia modesta*. A Beckman oxygen macroelectrode attached to a DC Null Voltmeter and a chart recorder was used. Specimens were placed in a 10 mL flask of filtered sea water containing an autonomic stirrer. The tests were conducted in an Econaire Growth Chamber which provided

a uniform temperature of 23°C and even illumination on all sides. The specimens were exposed to varying time periods (recorded in Figures 3 and 4) of light and dark and 0.9 g of *Elysia chlorotica* and 0.06 g of *Alderia modesta* were used. As an additional test of photosynthetic activity, inhibition of O_2 production was attempted by adding 3(3,4-dichlorophenol)-1, 1-dimethylurea (DCMU) ($4 \times 10^{-5} \text{ mol l}^{-1}$) to the *Elysia chlorotica* flask.

To compare overall pigment contents, approximately 1 g each of *Alderia modesta*, *Elysia chlorotica*, and *Vaucheria* sp. was crushed with 10 mL of cold acetone for 15 min. The resulting 3 crude extracts were filtered and the overall absorption spectra determined on a Varian Techtron UV-VIS Spectrophotometer.

OBSERVATIONS

Alderia modesta

The digestive diverticula of *Alderia modesta* branch off the large stomach and pass dorsally into the cerata and ventrally into the foot region. These digestive tubules are lined with epithelium supported by a thin layer of connective tissue. Smooth muscle bundles also envelop the tubules. A basement membrane was not observed. Chloroplasts are frequently present in the lumina of the tubules.

With light microscope techniques, two cell types form the epithelial lining (Figure 6). Cell type AI (*Alderia* I) is large and granular, whereas cell type AII (*Alderia* II) is small and non-granular. Cell AI is the more numerous and forms the lining of much of the tubule. With the hematoxylin and eosin and Mallory's methods, cell AI contains clear vacuoles and acidophilic granules while cell AII stains basophilically. Histochemically, both cells stain positively for glycogen, RNA, neutral lipids and both cells stain negatively for acid mucopolysaccharides and calcium. Acid phosphatase is present along the luminal

Explanation of Figures 6 to 11

Figure 6: Digestive tubule of *Alderia modesta* showing cell types AI and AII. Toluidene Blue O. $\times 1500$

Figure 7: Digestive tubule of *Elysia chlorotica* showing cell types EI and EII. Toluidene Blue O. $\times 1500$

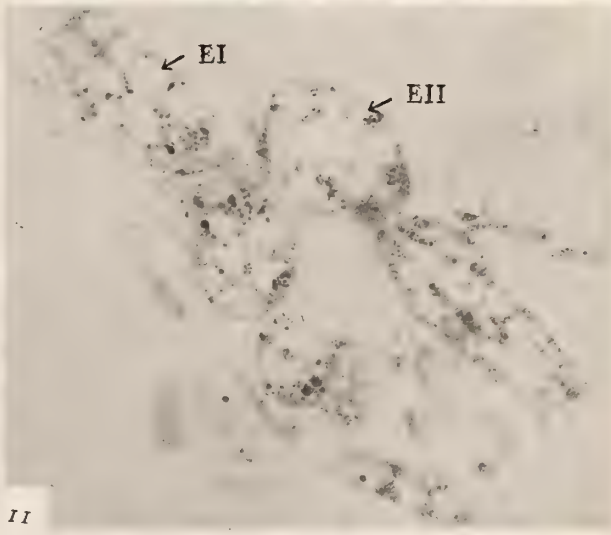
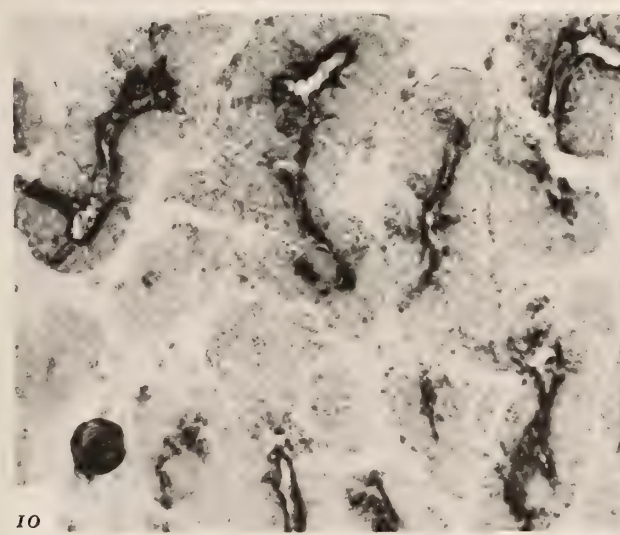
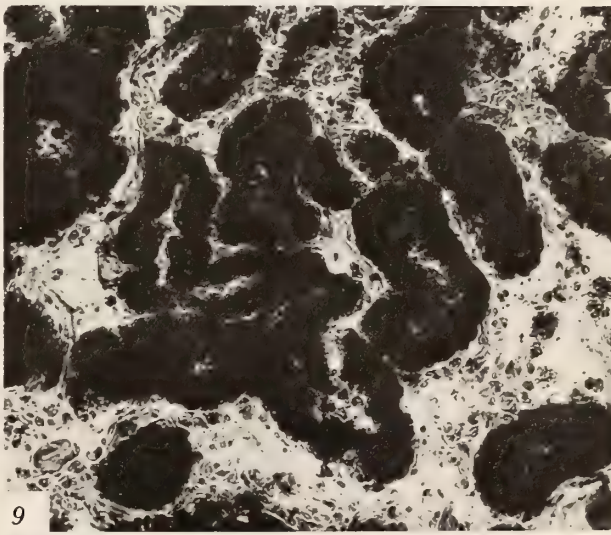
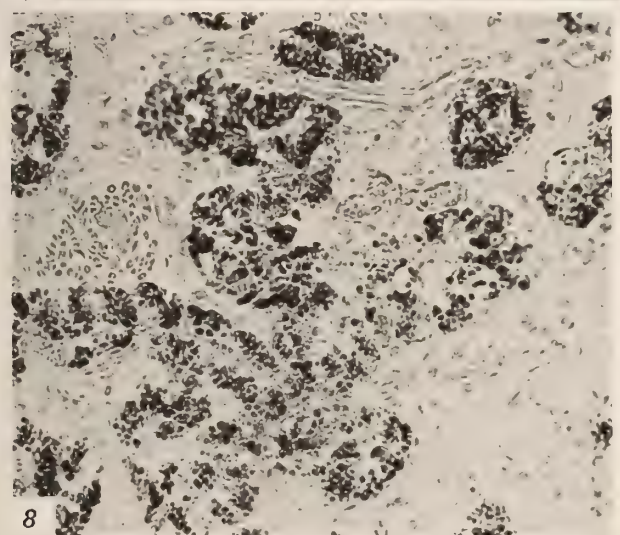
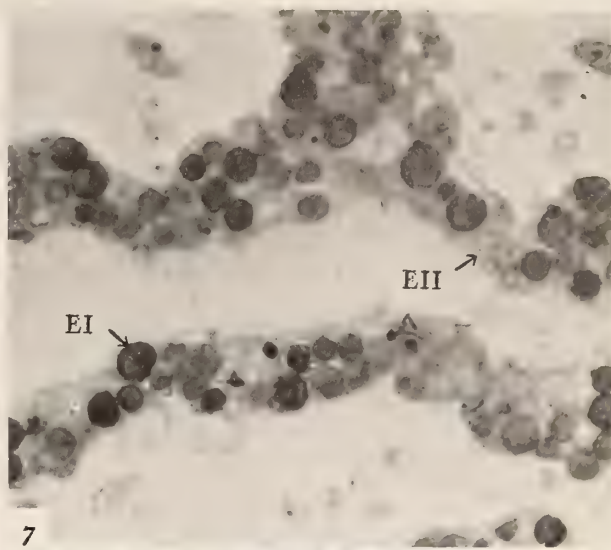
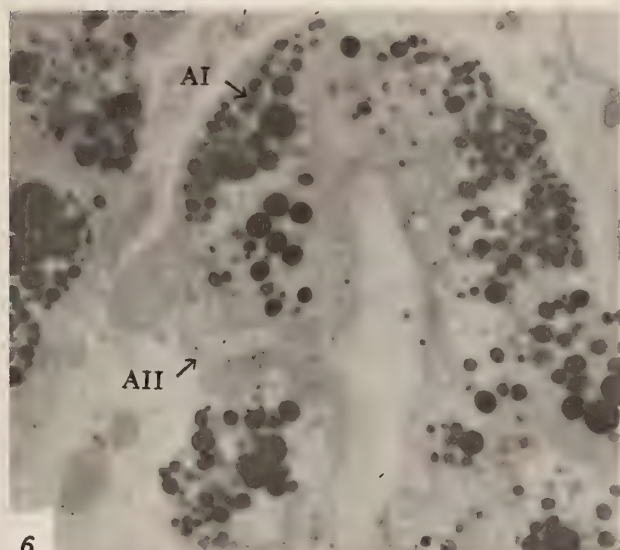
Figure 8: Digestive tubules of *Elysia chlorotica* showing staining reaction for neutral lipid. Oil Red O. $\times 375$

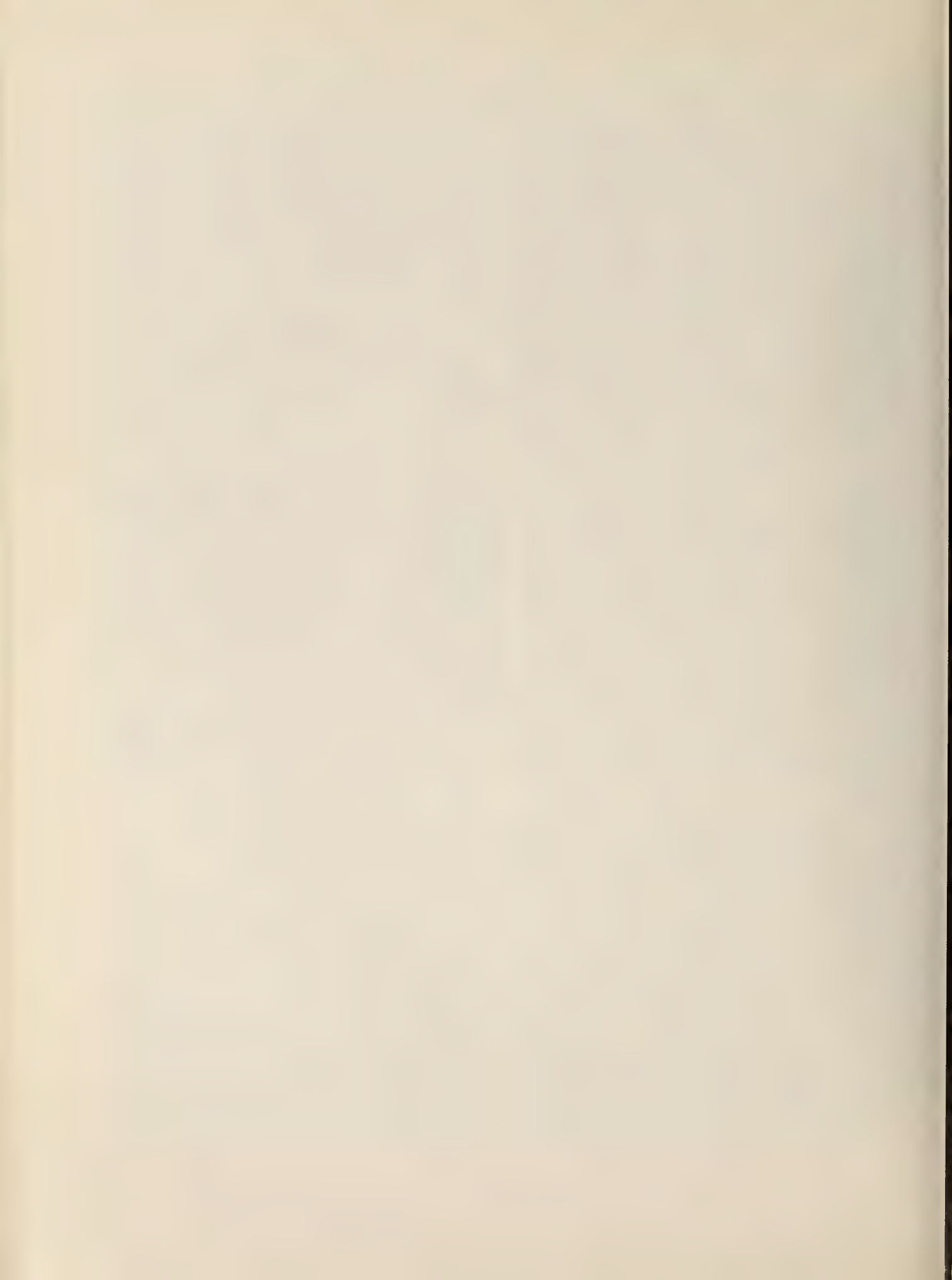
Figure 9: Digestive tubules of *Elysia chlorotica* showing staining

reaction for alkaline phosphatase. Gomori's method. $\times 375$

Figure 10: Digestive tubules of *Elysia chlorotica* showing staining reaction for alkaline phosphatase along the luminal border. Gomori's method. $\times 375$

Figure 11: Digestive tubules of *Elysia chlorotica* showing staining reaction for calcium (arrows). Note cell EI is negative and cell EII is positive. Alizarin. $\times 600$





border of both cell types. These staining reactions are summarized in Table 1.

Table 1

Staining affinities of the cell types in the digestive diverticula of *Alderia modesta* and *Elysia chlorotica*.

Staining Technique	Cell Types			
	<i>Alderia modesta</i> AI	<i>Alderia modesta</i> AII	<i>Elysia chlorotica</i> EI	<i>Elysia chlorotica</i> EII
PAS	*	*	*	*
methyl green-pyronin Y	*	*	*	*
oil red O	*	*	*	*
propylene glycol	*	*	*	*
Alcian blue	—	—	—	—
alizarin red S	—	—	—	*
acid phosphatase	*	—	**	—
alkaline phosphatase	**	**	**	**

— no reaction

* some reaction

** strong reaction

At the electron microscope level, the most diagnostic components of cell AI (Figures 1 and 12) are the heterogenous bodies. The heterogenous bodies are generally found in the apical half of the cell, each is encircled by a membrane, and each contains granules which may be loosely to densely packed. Chloroplasts are frequently observed in these cells. When present, they are surrounded by an extrinsic membrane and show varying degrees of degradation. Small vesicles are often found close to the chloroplasts and heterogenous bodies. Lipid inclusions are common, vary in size, and often are surrounded by heterogenous bodies. These cells have long or oval mitochondria, a rough endoplasmic reticulum usually located along the cell periphery and around the cell organelles, and a nucleus which frequently contains a rod-shaped crystal. Microvilli and many small vesicles are found along the luminal border and cilia are occasionally present.

Cell AII (Figures 1 and 13) is usually observed in the basal half of the epithelial lining. It contains long thin mitochondria, small vesicles, and glycogen. Concentric layers of smooth endoplasmic reticulum are prominently distributed throughout the cell. Lipid inclusions coupled with clear vesicles, vesicles containing material with a dense core, and cytoplasmic lattice-work crystals are pres-

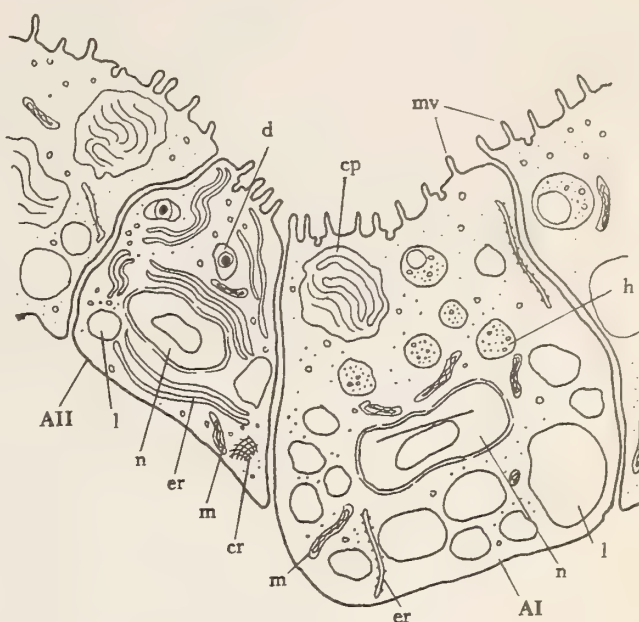


Figure 1

Diagrams of cell types AI and AII lining the digestive diverticula of *Alderia modesta*. cp—chloroplasts; cr—crystals; d—dense vesicles; er—endoplasmic reticulum; h—heterogenous body; l—lipid; ls—lysosome; m—mitochondria; mv—microvilli; n—nucleus

ent. The nucleus was not observed to contain crystals. Microvilli are present on those cells which extend to the luminal border.

Elysia chlorotica

The digestive diverticula of *Elysia chlorotica* arise from the small stomach as two ducts which immediately subdivide into many small tubules and ramify throughout the entire animal. Unlike *Alderia modesta*, *E. chlorotica* does not possess cerata. The tubules are lined with epithelium enveloped only with smooth muscle. A subepithelial basement membrane and connective tissue tunic could not be demonstrated. Unlike *A. modesta*, the lumina of the digestive diverticula of *E. chlorotica* are characteristically devoid of chloroplasts.

At the light microscope level, the epithelial lining contains 2 cell types, cell EI (*Elysia* I) and cell EII (*Elysia* II). With the histological techniques used, cell EI is cuboidal and contains acidophilic granules and cell EII is narrow, non-granular and stains basophilically (Figure 7).

Histochemically, both cells stain positively for glycogen, RNA, and neutral lipids (Figure 8). Acid mucopolysaccharides could not be demonstrated. Acid phosphatase is present in cell EI (Figure 9). Alkaline phosphatase occurs along the luminal border of both cells (Figure 10). The alizarin red S method demonstrates calcium granules in cell EII (Figure 11) and the Gomori method for alkaline phosphatase demonstrates extracellular calcium spherules throughout the animal. These staining reactions are summarized in Table 1.

At the electron microscope level, cell EI (Figures 2, 14 and 15) contains chloroplasts and cell EII does not. The chloroplasts are distributed throughout the cell and have an average diameter of $5.4\ \mu\text{m}$. They are bounded by an intrinsic double membrane, are composed of parallel lamellae and a homogenous matrix containing a few strands of lamellae. Small bodies, possibly oil droplets, may be present between the lamellae. Occasionally, this lamellar structure is not well defined and the chloroplasts appear to be degrading. Lipid inclusions, glycogen, mitochondria, and smooth endoplasmic reticulum are distributed throughout the cell. Large, often irregular shaped, clear or granular vesicles are occasionally present. The nucleus, often triangular in shape, is located in the apical half of the cell. The luminal border has many microvilli and a few cilia. Numerous small round vesicles, probably pinocytotic vesicles, many containing granules, are distributed throughout the apical cytoplasm and may also be located deeper in the cell.

Cell EII (Figures 2 and 15) occurs with the same frequency as cell EI. It is a narrow cell, having the nucleus situated in the apical half. The cytoplasm contains lightly stained granular material. Glycogen, small mitochondria, smooth endoplasmic reticulum, and granular vesicles which are presumably calcium spherules are found through the cell. Occasionally, Golgi bodies are observed. Lipid inclusions are found in the basal region of the cell.

The apical border has microvilli, a few cilia, and sub-jacent small pinocytotic vesicles.

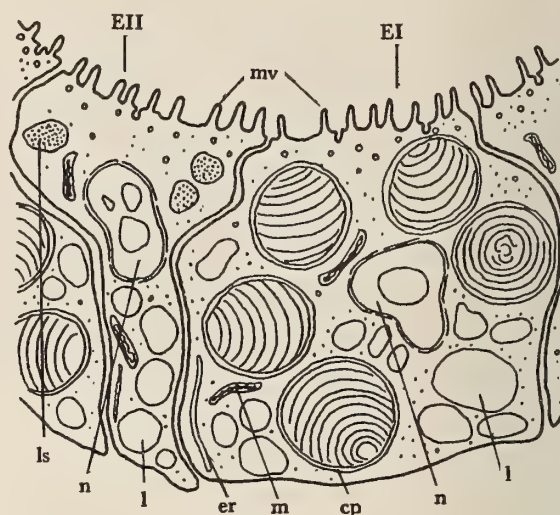


Figure 2

Diagrams of cell types EI and EII lining the digestive diverticula of *Elysia chlorotica*. Abbreviations as in Figure 1

Photosynthesis

The tests for photosynthetic activity with *Elysia chlorotica* show an increase in PO_2 when the flask was illuminated and a PO_2 decrease when the flask was darkened (Figure 3). The addition of DCMU to the flask containing *E. chlorotica* caused a decrease in PO_2 similar to that caused by the absence of light. Tests using *Alderia modesta* demonstrated that the presence of light did not influence the PO_2 level in the flask (Figure 4).

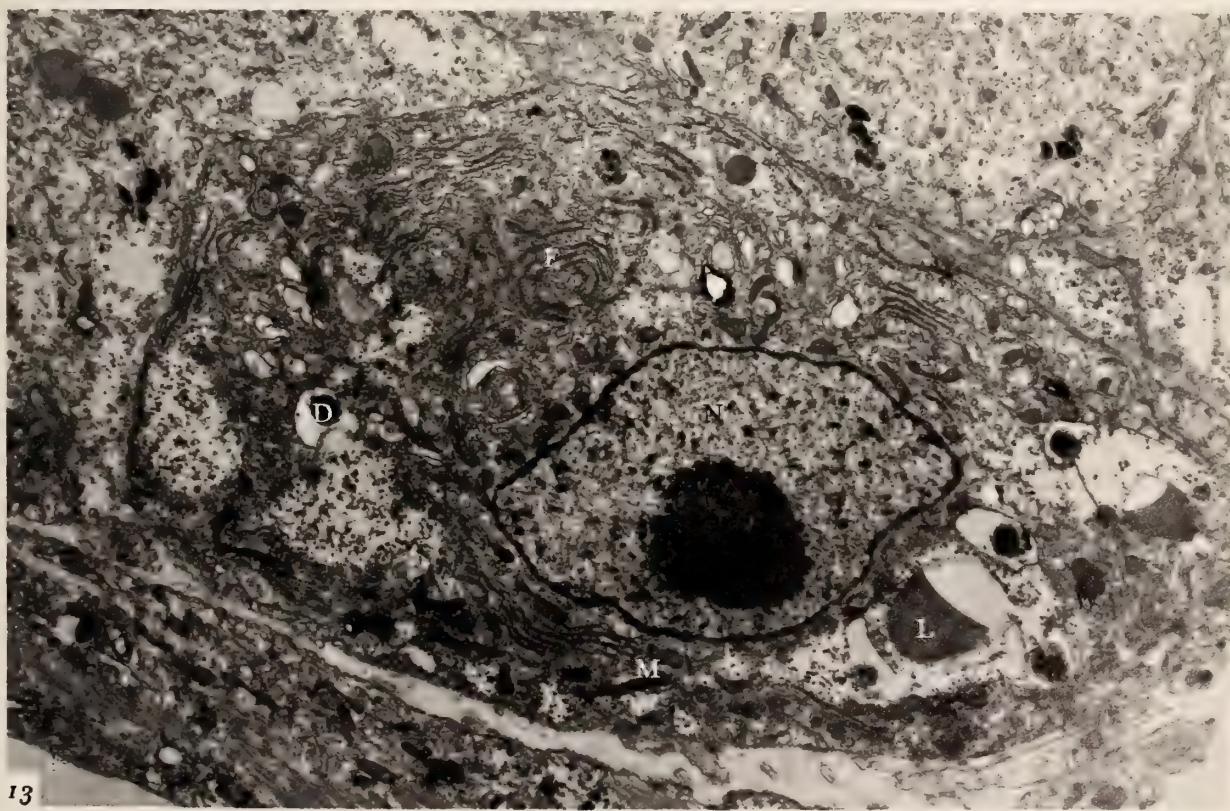
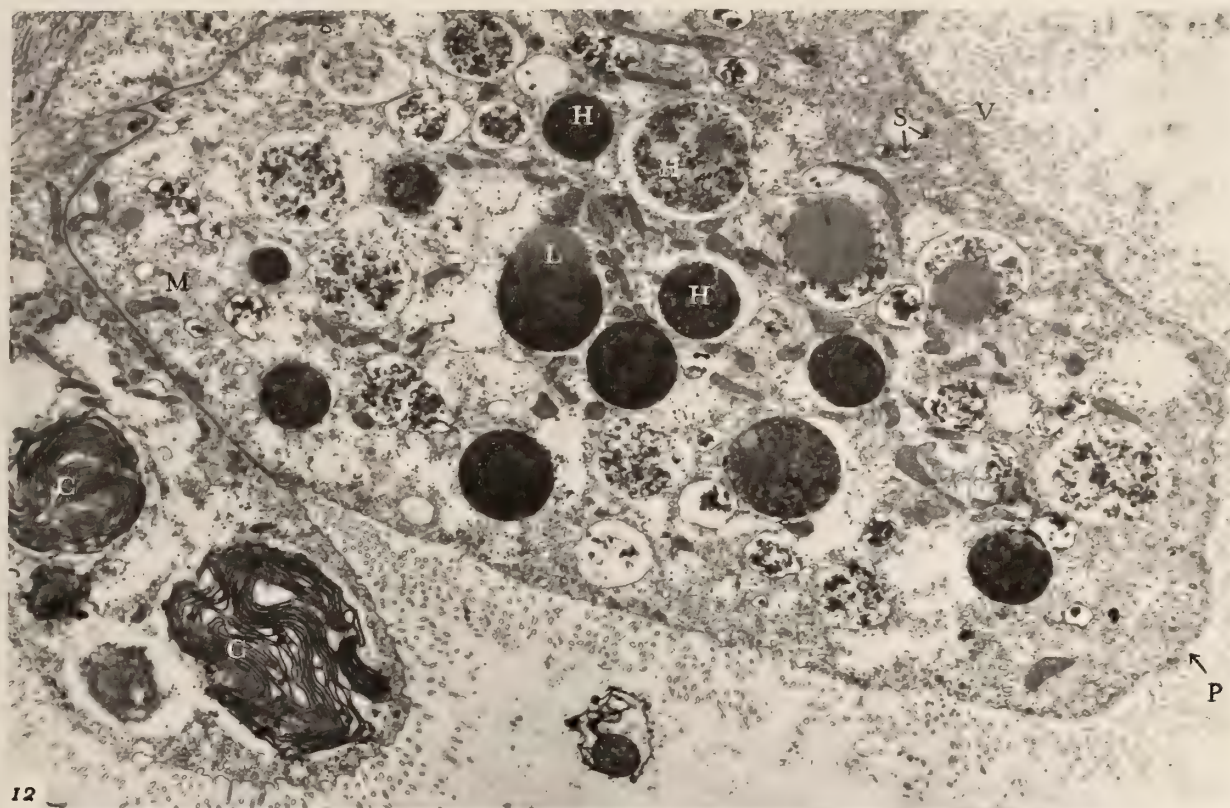
Explanation of Figures 12 and 13

Figure 12: Digestive tubule of *Alderia modesta* showing portions of two AI cells containing loosely and densely packed heterogeneous bodies (H), degraded chloroplasts (C), lipid (L) within heterogeneous body, mitochondria (M), microvilli (V), small vesicles (S), and pinocytotic activity (P). Uranyl acetate and lead citrate.

× 6 120

Figure 13: Digestive tubule of *Alderia modesta* showing AII cell. Mitochondria (M); endoplasmic reticulum (E); lipid (L) inclusions coupled with clear vesicles; vesicles containing material with a dense core (D); lattice-work crystals (W); and nucleus (N). Uranyl acetate and lead citrate.

× 7 600





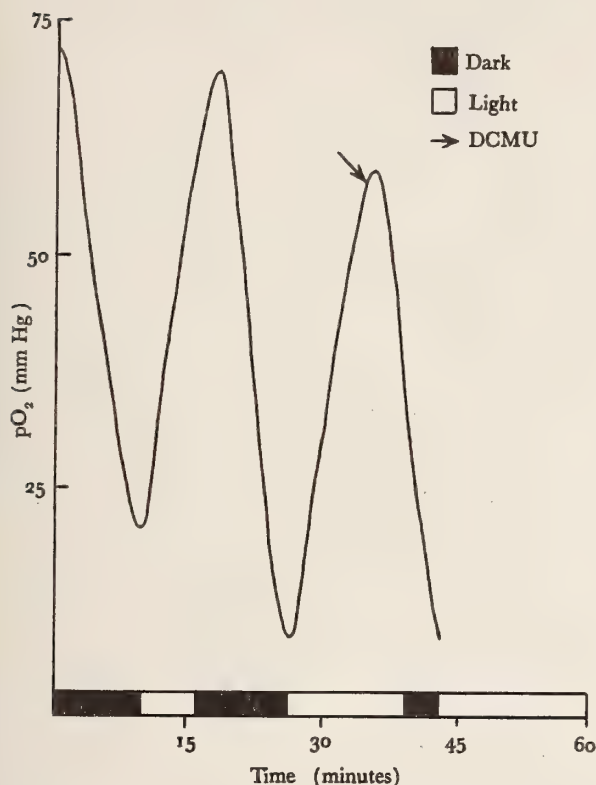


Figure 3

Graph showing oxygen release by *Elysia chlorotica* during light and dark periods and following administration of DCMU

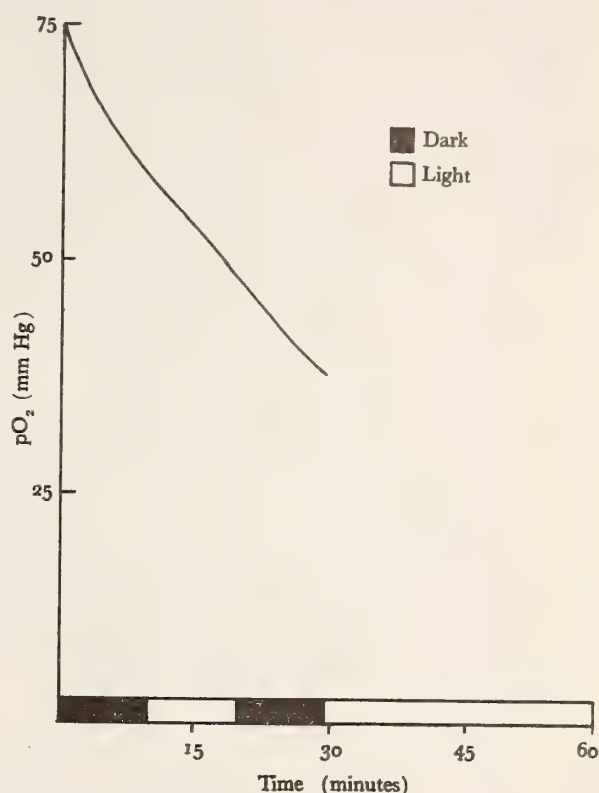


Figure 4

Graph showing oxygen release by *Alderia modesta* during light and dark periods

Pigment Analysis

As shown in Figure 5, the crude acetone extracts of *Elysia chlorotica* and *Vaucheria* sp. show absorption maxima at 370, 410, 425, 470, 570, 610 and 660 nm. The maxima for *Alderia modesta* are at 408, 442, 470, and 660 nm, but are not as high nor as distinct as those of *E. chlorotica* and *Vaucheria* sp.

DISCUSSION

HISTOLOGY

The digestive tubules of *Alderia modesta* are lined with epithelium supported by connective tissue and smooth muscle layers. A basement membrane was not observed.

The epithelial lining of *Elysia chlorotica* is surrounded by a smooth muscle layer, but no basement membrane or connective tissue layer was observed. The subepithelial layer of *E. viridis* contains a thick basement membrane and connective tissue layer (TAYLOR, 1968), while that of *E. atroviridis* has a thick basement membrane and both connective tissue and muscle layers (KAWAGUTI & YAMASU, 1965). The lumina of the diverticula of *E. chlorotica* are devoid of chloroplasts. A similar observation has been reported for *E. viridis* (TRENCH *et al.*, 1973). The lumina of *Alderia modesta*, on the other hand, characteristically contains chloroplasts. This suggests that *A. modesta* feeds regularly, whereas *E. chlorotica* feeds only sporadically, obtaining energy from the photosynthetic activity of its intracellular chloroplasts.

The digestive diverticula of *Alderia modesta* are lined by 2 epithelial cell types. Cell AI is the larger, is more

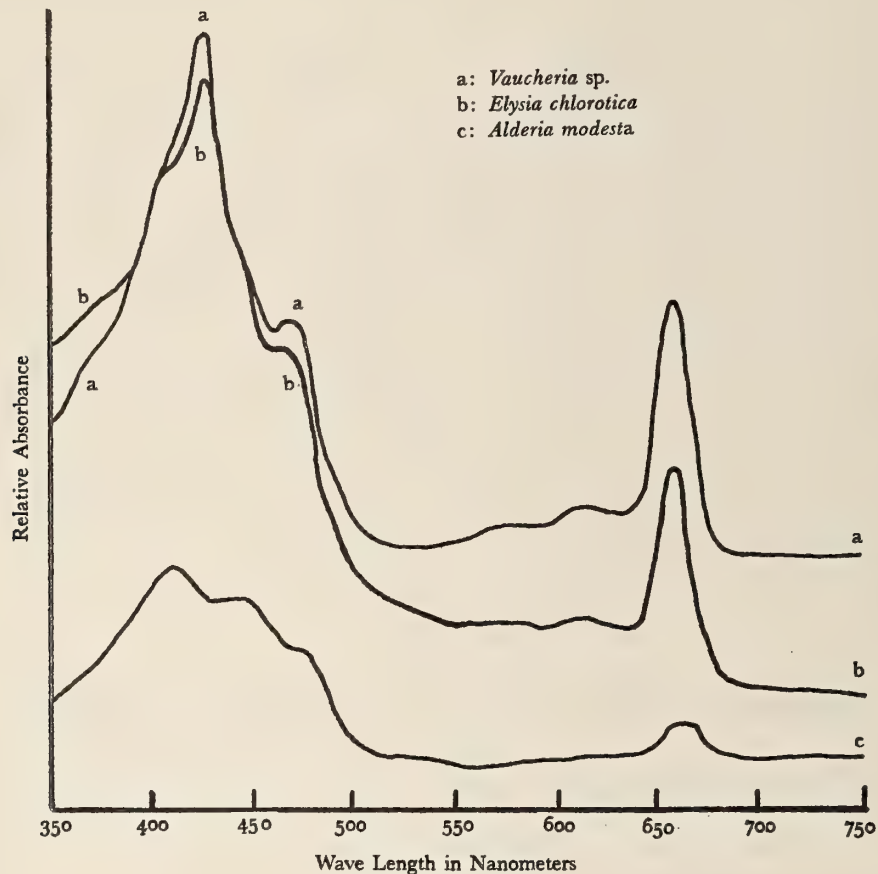


Figure 5

The absorption spectra of crude acetone extracts from tissues of *Vaucheria* sp., *Elysia chlorotica* and *Alderia modesta*

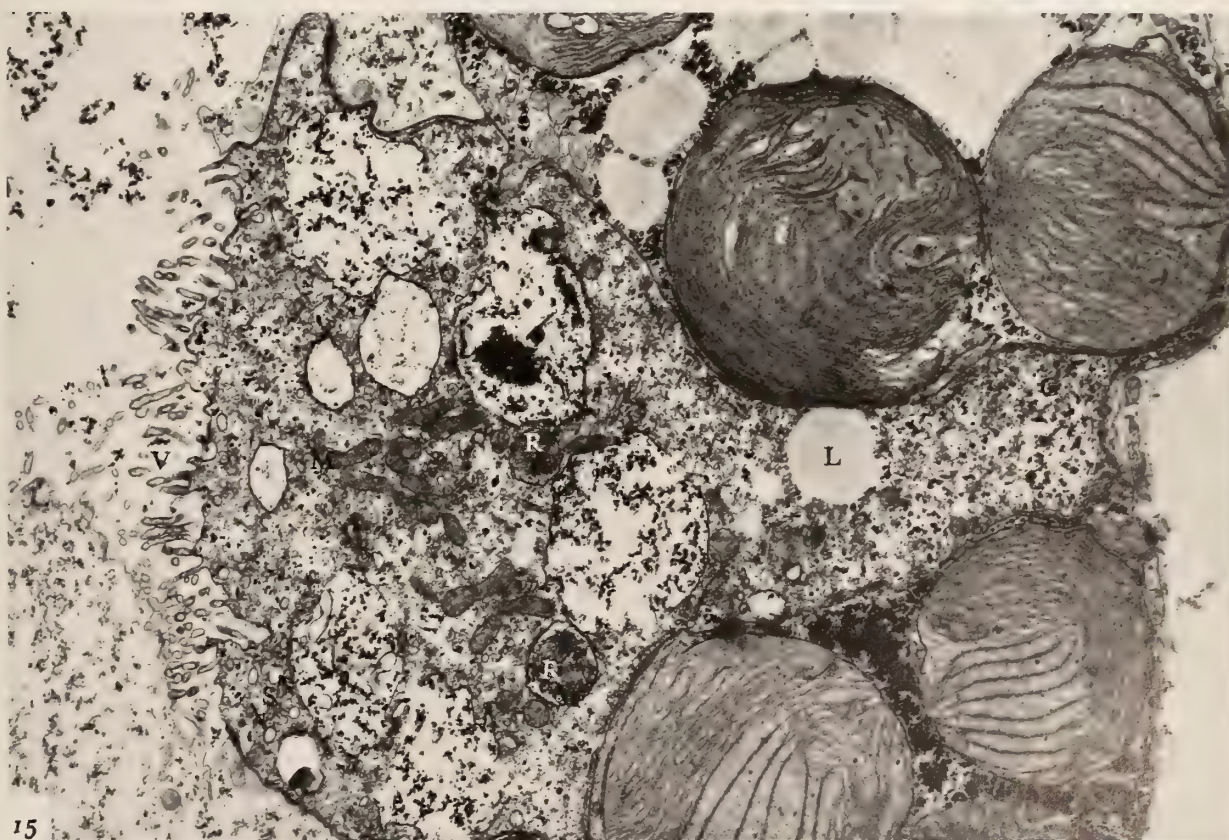
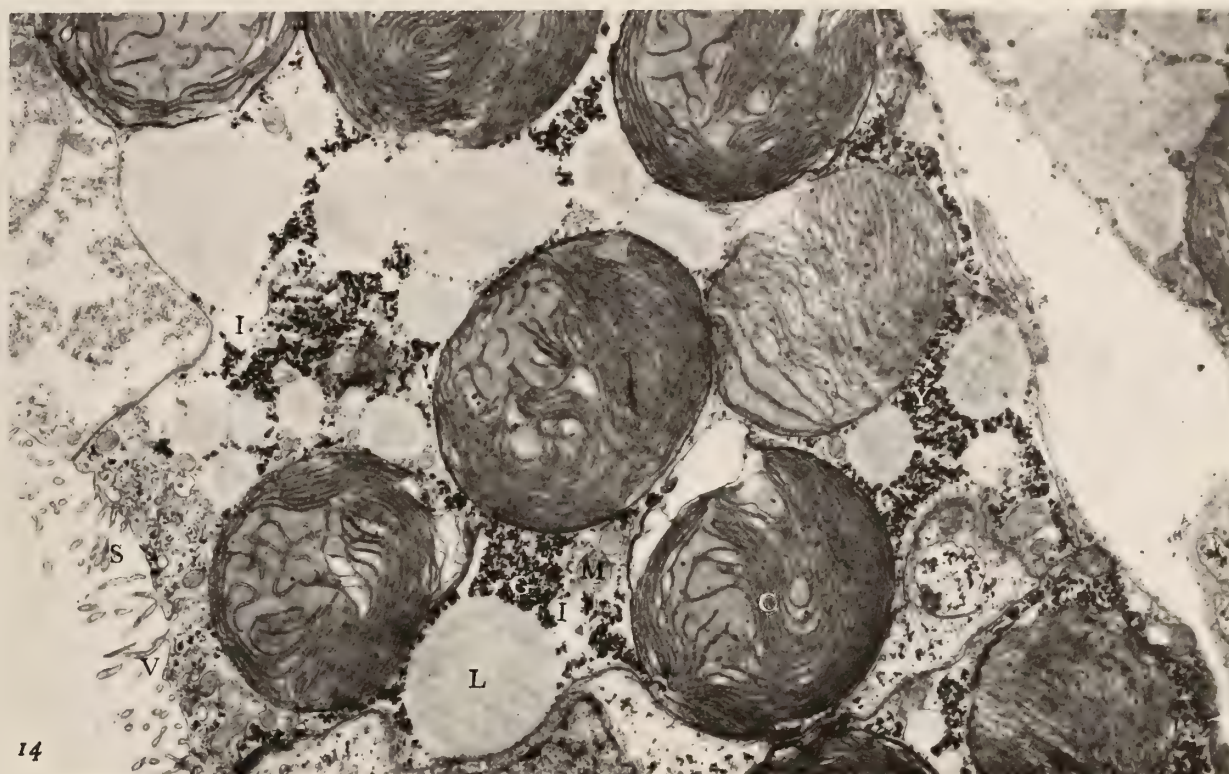
numerous, and possesses a granular cytoplasm. It is suggested that this cell has a digestive function because it stains positively for acid phosphatase, an enzyme associated with lysosomes. Also, the luminal border stains intensely for alkaline phosphatase, indicating the presence of microvilli and suggesting a border which is active in

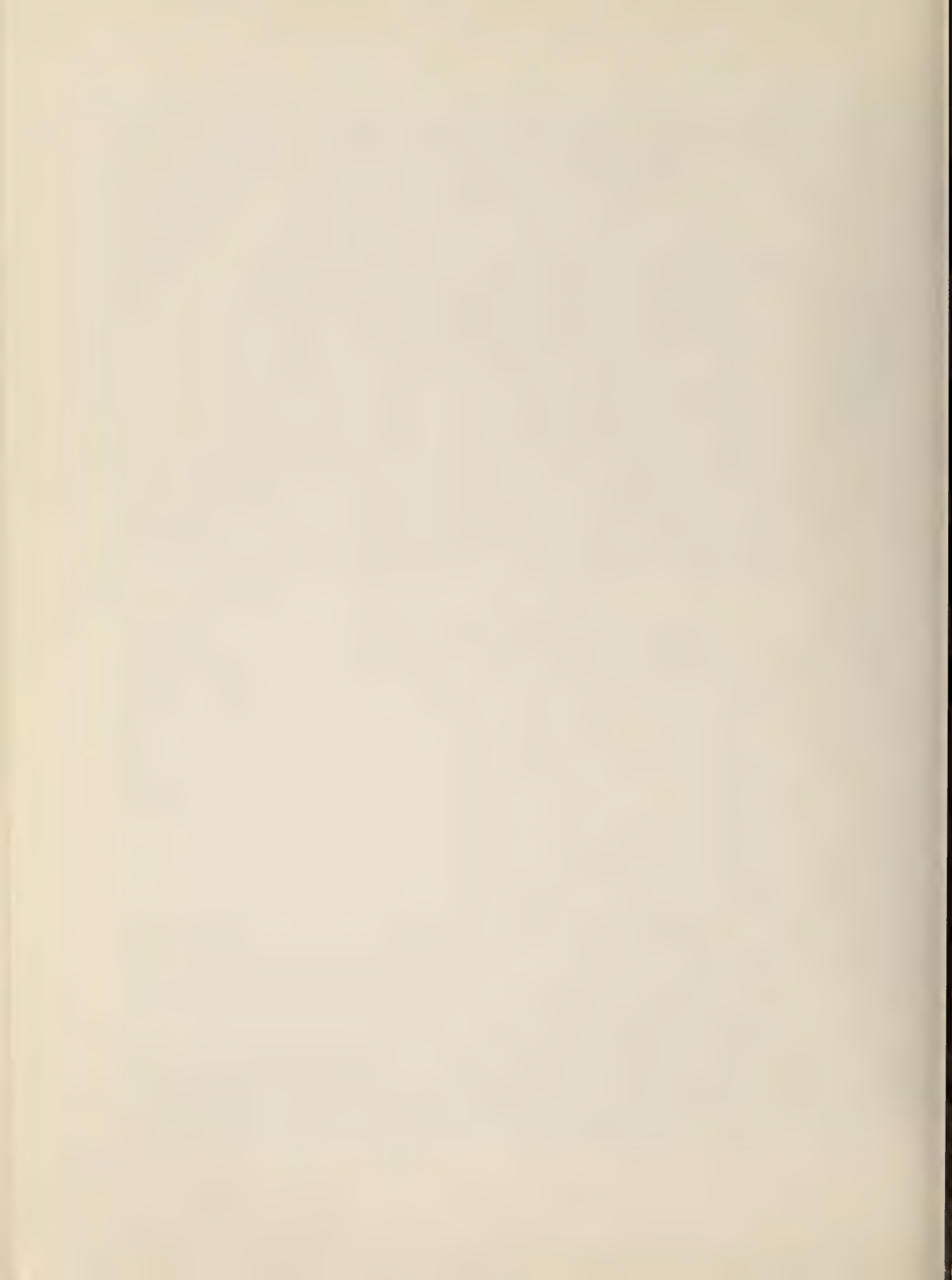
transport. Ultrastructurally, this cell contains chloroplasts in various stages of degradation surrounded by an animal cell membrane, presumably a phagosome. MUSCATINE *et al.* (1975) proposed that chloroplasts within vacuolar membranes are subject to hydrolysis by lysosomes, whereas symbiotic chloroplasts occur free in the sacoglossan

Explanation of Figures 14 and 15

Figure 14: Digestive tubule of *Elysia chlorotica* showing EI cell with intact chloroplasts (C); glycogen granules (G); lipid inclusions (L); mitochondria (M); irregularly shaped vesicles (I); microvilli (V); and small vesicles along luminal border (S). Uranyl acetate and lead citrate. $\times 6120$

Figure 15: Digestive tubule of *Elysia chlorotica* showing EII cell between two EI cells. Glycogen (G); mitochondria (M); granular vesicles or lime spherules (R); lipid (L); microvilli (V); and small vesicles along luminal border (S). Uranyl acetate and lead citrate. $\times 7200$





digestive cell cytoplasm and are thereby protected from enzymatic degradation. During degradation, chloroplasts of *A. modesta* lose their original shape and the lamellae become indistinct. Often small vesicles are associated with the chloroplasts. The heterogenous bodies, typical of the AI cell, are possibly vesicles of chloroplast digestion. Some of the small vesicles associated with both the chloroplasts and the heterogenous bodies may be lysosomes. Others may be pinocytotic vesicles from the luminal border. Presumably, phagocytosis also occurs as chloroplasts are often observed under the luminal border. However, the process of phagocytosis as described by McLEAN (1976) for another eolidiform sacoglossan, *Placida dendritica*, was not seen.

Cell AII is smaller and less numerous than cell AI and, histochemically, it differs from AI in that it does not exhibit a positive reaction for acid phosphatase. At the electron microscope level, cell AII contains some distinct inclusions: vesicles having a dense core, lattice-work crystals, and an extensive endoplasmic reticulum. The function of this cell is unknown. However, the extensive endoplasmic reticulum and the pinocytotic or endocytotic activity of the luminal border indicate a very active cell. Also, the intense alkaline phosphatase activity along the luminal border indicates active transport. Thus, it appears that this cell is either secreting into the lumen or sequestering substances from the lumen.

The epithelial lining of the digestive diverticula of *Elysia chlorotica* also has 2 cell types, cell EI and cell EII. Cell EI is cuboidal in shape and contains acidophilic granules. FRETTER (1940) reported a cell showing a similar histology in *E. viridis* except that the cell she described contained vacuoles of yellowish or brown material which she suggested were excretory masses derived from the digestion of food. TAYLOR (1968) also described the granular cells in *E. viridis* which contained the excretory masses. The cell in *E. viridis* contains acid mucopolysaccharides, otherwise it is histochemically similar to the one reported in the present study. It is suggested that cell EI is digestive in function as it exhibits an intense acid phosphatase reaction indicating the presence of lysosomes, and an intense alkaline phosphatase reaction along the luminal border indicating active transport. The presence of microvilli and pinocytotic vesicles supports this suggestion. Fretter and Taylor also refer to this cell type in *E. viridis* as a digestive cell.

At the electron microscope level EI of *Elysia chlorotica* is comparable to the digestive cell of *E. viridis* as described by TAYLOR (1968). However, certain differences are evident. The chloroplasts of *E. chlorotica* differ in size and structure from those of *E. viridis*. Those in *E. chlorotica* possess a lamellar structure and a region of homo-

genous matrix containing a few strands of lamellae. They have a mean diameter of $5.4\text{ }\mu\text{m}$. Only the chloroplast envelope was observed, which supports the conclusions of MUSCATINE *et al.* (1975) that active chloroplasts are in direct contact with the host's cytoplasm and that only defunct chloroplasts in *Elysia* spp. become enveloped by autophagic host vacuoles. The chloroplasts of *E. viridis*, from the siphonaceous alga *Codium fragile*, are $2 - 3\text{ }\mu\text{m}$ in diameter and possess a lamellar structure of double disc bands, oil droplets and a discoidal starch grain. The large clear digestive vacuoles of *E. viridis* are not present in *E. chlorotica*. However, numerous lipid inclusions are present and are large and lightly stained.

Cell EII is a long narrow cell, less common than cell EI, and stains basophilically. This cell stains positively for calcium and appears to be similar to the lime cell in *Elysia viridis* described by TAYLOR (1968) which is also positive for calcium. Both FRETTER (1940) and TAYLOR (*op. cit.*) suggest that this cell type may have a buffering function. At the electron microscope level, the lime cells of *E. chlorotica* and *E. viridis* appear to be similar. Both cells lack chloroplasts and contain electron dense lime vesicles. The large lipid inclusions found in the basal region of the *E. chlorotica* lime cell are comparable to the large vacuoles often found in the lime cell of *E. viridis*. Pinocytotic or endocytotic activity is present along the luminal border of the lime cells in both species.

Thus, at the electron microscope level, the 2 cell types in *Elysia chlorotica* correspond closely with the digestive and lime cells of *E. viridis* as reported by TAYLOR (1968).

Photosynthesis

Studies of O_2 production undertaken to test *Elysia chlorotica*'s capacity for photosynthesis showed that these animals are capable of producing an increase in the PO_2 of the surrounding water when supplied with sufficient light. This major increase in the water PO_2 to the level of saturation of the chamber and consequent formation of O_2 bubbles, could only be caused by photosynthesis of chloroplasts in the digestive cells. The PO_2 levels in the flask containing *Alderia modesta* were not influenced by light, indicating that the chloroplasts of *A. modesta* are not photosynthetically active. This is in agreement with HINDE & SMITH (1974).

Pigment Analysis

Spectral analysis of the acetone-extracted pigments reveals that the absorption maxima of *Elysia chlorotica* and the alga *Vaucheria* sp. are the same, indicating that *Vaucheria* sp. is the food plant of *E. chlorotica*. Although *Al-*

deria modesta is known to eat *Vaucheria* sp. (EVANS, 1953) and is found on *Vaucheria* sp. in the Minas Basin region, the absorption maxima of *A. modesta* are similar but not identical to those of *Vaucheria* sp. This indicates that chloroplast pigments are broken down soon after ingestion. HINDE & SMITH (1974) reported that chlorophyll degradation is probably rapid in *A. modesta*.

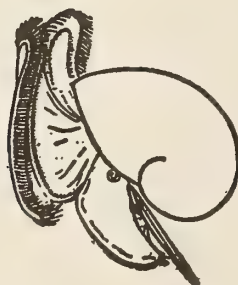
SUMMARY

Although *Alderia modesta* and *Elysia chlorotica* occupy similar habitats and feed on the same alga, they differ with respect to the structure of their digestive diverticula and their mode of nutrition. The majority of the cells lining the diverticula of *A. modesta* are involved with rapid degradation of the algal cell contents, including chloroplasts, whereas much of the epithelial lining of the diverticula of *E. chlorotica* is involved with the long term retention of photosynthetically active chloroplasts.

This discovery of active chloroplasts of *Vaucheria* sp. in the digestive cells of *Elysia chlorotica* is the first evidence of a symbiotic relationship between an elysiid sacoglossan and an alga of the Order Xanthophyta.

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Notes on the Reproductive Strategies of the South African Vermetid Gastropods *Dendropoma corallinaceum* and *Serpulorbis natalensis*

BY

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INTRODUCTION

THE PRESENT PAPER discusses the adaptive significance of the reproductive methods employed by *Dendropoma corallinaceum* (Tomlin, 1939) and *Serpulorbis natalensis* (Mörch, 1862) in the light of new data on juvenile respiration rates, energy reserves and dispersal capabilities, together with the general biological information on these species described in HUGHES (1978a, 1978b).

Dendropoma corallinaceum is a dominant organism of exposed rock faces in the cooler waters of the Cape Province of South Africa, being replaced by a very similar species, *D. tholia* Keen & Morton, 1960, in warmer waters from the Transkei northwards. *Dendropoma corallinaceum* builds sheet-like colonies over the rock surface and on vertical faces the colonies form a zone about 1 m wide centred on LWS. Upper limits to this zone are set by desiccation and lower limits are often set by competition with the limpet *Patella cochlear* Born, 1778. *Serpulorbis natalensis* has the same geographical distribution as *D. corallinaceum* but occurs in loose aggregations beneath stones and on the sides of boulders below LWS in fairly sheltered water. It is replaced by the broadly similar species *S. aureus* Hughes, 1978 (HUGHES, 1978c) in the Transkei.

MATERIALS AND METHODS

During August–November 1975, *Dendropoma corallinaceum* and *Serpulorbis natalensis* were kept in the laboratory, during which time they produced large numbers of young, making it possible to measure juvenile respiration rates and to collect material for subsequent biochemical analysis. From these observations it was possible to esti-

mate the energetic cost of the pre-settlement dispersal phase and to compare this with the energy reserves of the newly hatched young.

ANIMALS

Dendropoma corallinaceum was collected from the upper edge of the *Patella cochlear* zone (MLW) at Miller's Point on the Cape Peninsula. Lumps of the reef-like colonies were chipped off the rock face and placed in a well-aerated aquarium at ambient air temperature. Crawling young emerged from the colonies within 24 h but the hatching rate declined over several weeks. The adults survived and sustained normal feeding activities for 4 months. *Serpulorbis natalensis* were collected from the undersurfaces of stones within 1 m below MLW on the southern (lee) side of Schaapen Island, Langebaan. Crawling young emerged within 24 h, continuing to emerge for 2 weeks.

The aquarium was cleared of young at 21:00 h and the freshly hatched young that had accumulated by 08:00 h the next morning were collected and placed in the respirometer.

RESPIROMETRY

A Gilson differential respirometer was used. For both species a set of 4 experimental flasks with 2 control flasks was run with KOH as the CO₂ absorbant. Each experimental flask contained 40 *Dendropoma corallinaceum* or 23 *Serpulorbis natalensis* in 2 mL filtered seawater. The control flasks were similar to the experimental flasks but lacked animals. The apparatus was kept at 15.5°C, close to the prevailing sea temperature and the flasks were gently shaken. After the animals were introduced, the ap-

paratus was allowed to equilibrate for 1 h. Readings were then taken every 3 h for a total of 15 h.

BIOCHEMICAL ANALYSIS

Newly hatched juveniles were fixed in 5% saline formalin for transportation to the United Kingdom. The fixed samples of larvae complete with protoconchs were washed in 0.9% aqueous ammonium formate to remove seawater without changing the osmotic pressure, and freeze-dried. They were then comminuted in a vibrating ball mill. Carbohydrate and lipid contents were determined, as described previously by HOLLAND & HANNANT (1973). Protein was determined in a sample of the initial aqueous homogenate by the method of LOWRY, ROSEBROUGH, FARR & RANDALL (1951). Total dry weights were measured individually on a Cahn electrobalance after drying at 60°C for 48 h. Ash contents were weighed after roasting at 500°C for 4 h in platinum crucibles.

RATES OF SINKING

In order to test potentiality of juveniles being carried by water currents, the rates of sinking of newly hatched juveniles were measured, using a 40 cm column of 38‰ seawater at 18°C and a stop-watch.

RESULTS

RESPIROMETRY

Respiration rates remained steady throughout the 15 h experiment with no evidence that O₂ became limiting.

At the termination of the experiment the young snails were still active and apparently healthy. The O₂ consumption rate corrected to STP was 0.11 µL per individual (4.26 ± 0.25 µL per flask) for *Dendropoma corallinaceum* and 0.07 µL per individual (1.66 ± 0.07 µL per flask) for *Serpulorbis natalensis*.

BIOCHEMICAL ANALYSIS

Table 1 shows that about 35% of the total dry weight is due to protein. Carbohydrates account for less than 2% of the total dry weight. Neutral lipid, amounting to about 7-12% of the total dry weight, is the probable source of energy for the animals.

Newly hatched *Dendropoma corallinaceum* contain 5 µg neutral lipid, which is equivalent to 0.2 J energy (CRISP, 1971). Similarly, *Serpulorbis natalensis* contains 14.7 µg neutral lipid, equivalent to 0.06 J. Using an energy equivalent of 13.72 J mg⁻¹ O₂ STP liberated as heat during the catabolism of lipid (ELLIOTT & DAWSON, 1975), I estimate that *D. corallinaceum* loses 2.16×10^{-3} J h⁻¹ as heat and will therefore exhaust its lipid energy reserves in 4-5 days. *Serpulorbis natalensis* loses 1.37×10^{-3} J h⁻¹, so that its lipid will last about 18 days. Catabolism of the carbohydrate would sustain *D. corallinaceum* for a further 5-6 h and *S. natalensis* for a further day.

RATES OF SINKING

Dendropoma corallinaceum has a robust shell that sank at a rate of 3.2 cm sec⁻¹, S.E. = 0.02, n = 5. *Serpulorbis natalensis* has a lighter shell and unlike *D. corallinaceum* is variable in size. The rate of sinking was inversely proportional to size, small individuals of 0.7 mm shell length

Table 1

Biochemical composition expressed as percentage of total freeze dried weight (including shell). Individual total dry weights are the means of 6 replicates. Figures in parentheses are the proportions of total lipid, total carbohydrate and protein in the biochemically extracted material.

	Individual total dry weight µg	Ash content %	Neutral lipid %	Phospholipid %	Free Polysaccharide %	Free sugars %	Protein %
<i>Dendropoma corallinaceum</i> newly hatched juveniles	73 ± 9	55	6.8 (22)	0.6	0.9 (4)	0.1	35.5 (76)
<i>Serpulorbis natalensis</i> newly hatched juveniles	126 ± 20	50	11.7 (24)	0.2	1.3 (3)	0.3	35.6 (73)

sinking at 1.7 cm sec^{-1} , S. E. = 0.01, $n=5$ and large individuals of 1.4 mm shell length sinking at 1.0 cm sec^{-1} , S. E. = 0.01, $n=5$. The above sinking rates were observed for animals completely retracted within the shell. The sinking rate is reduced considerably when the animal extends its foot, and is reduced even further when a string of mucus is secreted. *Serpulorbis natalensis* reduced its sinking rate from 1.7 cm sec^{-1} with the foot retracted to 0.7 cm sec^{-1} with the foot extended. The sinking rate with a mucous "drogue" was very variable but was an order of magnitude less than the rates without mucus.

DISCUSSION

Because of lack of time and equipment, only a few data on respiration rates and very crude data on energy reserves could be obtained. These data cannot be used as precise estimations but they do enable qualitative deductions to be made about the reproductive strategies employed by *Dendropoma corallinaceum* and *Serpulorbis natalensis*.

ENERGY RESERVES

Lipid is the most efficient form of energy storage where size is limiting, as with the young of most marine invertebrates. Thus, HOLLAND *et al.* (1975) found that lipid is the major energy reserve of the veligers and developing embryos of *Littorina* spp. The same has been reported for oyster veligers (HOLLAND & SPENCER, 1973) and barnacle cyprids (HOLLAND & WALKER, 1975). The vermetids conform with this trend.

DISPERSAL

Dendropoma corallinaceum will settle on adult colonies within 24 h after hatching but can delay settlement up to 4 days in the absence of suitable substrata. The adult feeding method using a mucous web probably occurs only after the completion of metamorphosis 2 days after settlement (HUGHES, 1978a). These published observations on settlement and the present data on respiration rates and lipid stores both predict that a maximum of 4-5 days is available to the juvenile *D. corallinaceum* for dispersal. Metamorphosis will take a further 2 days, during which time the lipid energy reserve will be virtually exhausted. However, *D. corallinaceum* tends to settle on Lithothamnium-type alga that grows over the rocks and over the surfaces of adult colonies. The settling juvenile rasps out a groove in the Lithothamnium to accommodate the grow-

ing shell, during which time green faecal pellets are produced. Evidently some of the eroded Lithothamnium is ingested and may provide supplementary food during metamorphosis. There are no data on the settlement behaviour of *Serpulorbis natalensis*. The above estimates are minimal, assuming that lipid is the principal energy source during dispersal and metamorphosis and taking no account of leaching of material during fixation. Carbohydrate is too scarce to be an important energy source and we suppose that protein is nearly all used for growth and enzyme production, although some energy is probably derived from protein catabolism. It is impossible to measure the absolute dispersal capabilities of either species in the field, but an indication of their relative dispersal powers can be derived from the data at hand. *Dendropoma corallinaceum* crawls at a speed of $7.4 \text{ mm minute}^{-1}$, which is twice as fast as *S. natalensis* (HUGHES, 1978a). The higher activity rate of *D. corallinaceum* is reflected by its higher respiration rate, being about 1.6 times that of *S. natalensis*. Thus, on a random walk, *D. corallinaceum* should be able to crawl $\sqrt{2}$ times as far per day as *S. natalensis*. However, *S. natalensis* has energy reserves sufficient to last 4-5 times as long as *D. corallinaceum* and so should be capable of crawling much further than the latter species before settlement if suitable substrata are not encountered meanwhile.

The probability of any individual reaching a given distance will also depend on the mortality rate and cohort size. Little can be inferred about the mortality rates during dispersal except that *Dendropoma corallinaceum* lives on exposed shores where there is a danger of being dislodged by wave action, whereas *Serpulorbis natalensis* lives in calmer water below MLW and is less at risk to this danger. *Dendropoma corallinaceum* produces a single young per capsule, whereas *S. natalensis* releases about 24 young per capsule (HUGHES, 1978a). There is no information on relative development rates or on the lengths of breeding season (except that *D. corallinaceum* liberated young in the field during the entire study from July to November) but it seems likely that *S. natalensis* is much more fecund than *D. corallinaceum*.

So far we have assumed that juveniles disperse by crawling and are therefore limited to distances less than 10 m. It is possible that juveniles, having become detached from the substratum by wave action, are carried by water currents over much larger distances, depending on current speed and direction, turbulence and rate of sinking. The observed sinking rates show that *Dendropoma corallinaceum* must experience turbulence sufficient to carry even retracted individuals at least 10 m. Individuals with mucous drogues could be kept in suspension for several days and carried distances exceeding 100 or even 1000 m, de-

pending on currents. The sticky quality of the mucus would enhance reattachment should the disseminules be brought against a solid surface. However, the probability of a water-borne juvenile reattaching to a surface suitable for settlement must be very small, so that the majority of *D. corallinaceum* settling successfully will be those that have dispersed by crawling. Moreover, *D. corallinaceum* is highly gregarious, juveniles settling on any suitable place immediately outside the grazing ranges of the adults. Occasional individuals may succeed at long distance dispersal via water currents to found colonies elsewhere. The energy reserves will enable water-borne individuals to endure long distance dispersal, whereas quickly settling juveniles may be able to use the stored energy for more rapid metamorphosis and growth.

A similar general pattern of dispersal probably holds for *Serpulorbis natalensis*, except that smaller, looser colonies are formed. Long distance dispersal by water currents is possibly rarer; the calmer water will make detachment and suspension of the juveniles less frequent. Indeed, it is difficult to imagine how juveniles in calm water could become suspended. It is possible that *S. natalensis* sometimes produces planktonic veligers for long distance dispersal. The variability of hatching size has already been noted. HADFIELD *et al.* (1972) have shown for several Hawaiian vermetids that embryo size varies considerably within a species or even within single broods and that large embryos that have consumed more yolk from nurse cells hatch as crawling young, whereas smaller embryos that have consumed less yolk may be released as planktonic veligers.

REPRODUCTIVE STRATEGIES

Dendropoma corallinaceum exploits a habitat that is severe because of heavy wave action, but is stable in the sense that environmental conditions remain constant throughout time. By forming continuous sheet-like colonies *D. corallinaceum* has become eminently suitable for exploiting the continually wave-scoured rock faces. Within its zone, *D. corallinaceum* is completely dominant, excluding all other species that potentially compete for space. This competitive superiority is achieved by the dense packing of contiguous individuals, which allows almost the entire surface of the colony to be grazed free of intruding organisms. However, once *D. corallinaceum* has extended to the limits of its zone, the space available to settling larvae will be confined to those micro-patches on the surface of the colony which are beyond the reach of the grazing adults (grazing occurs sporadically and is used primarily for clearing fouling particles rather than for feeding, which normally makes use of a mucous net).

New patches available for settlement will become available as adults die. Sections through colonies show that most individuals reach adult size, relatively few dying at small sizes. The colony is not built up in layers but increases in thickness due to the upward spiral growth of adults and of juveniles that have settled gradually and sporadically over the surface of the colony. Space suitable for settling juveniles must be severely restricted and probably becomes available at a slow steady rate. The best strategy under these circumstances is to liberate gradually, over a protracted period, large juveniles that are robust and advanced enough to settle, metamorphose and grow quickly. The production of many juveniles, especially in pulses, would be disadvantageous because most of them would fail to find a vacant settlement site. Moreover, with a fixed parental energy income, the production of more young would reduce their individual size and hence their competitive ability. *Dendropoma corallinaceum* is a good example of a K-selected species (MACARTHUR, 1972) adapted to stable environmental conditions where the population remains close to an equilibrium density and competition (for space) is at a premium. As expected from the theory of r- and K-selection, *D. corallinaceum* has a protracted breeding season (at least from July to November), relatively low fecundity, but large young. These K-selected attributes are achieved at a cost of lowered potential rate of increase and dispersability. Unpredictable, density-independent mortality does strike *D. corallinaceum*. Old colonies that have become very thick are weakened and tend to slough off the rock in small patches. The effect is exacerbated by subsequent wave action that erodes the newly exposed edges of the colony. Dispersal to such newly bared rock is well within the capabilities of juveniles crawling from the surrounding colonies. However, settlement in such bare areas was never recorded in the field, probably because the rocks in the study area were too hard for the juveniles to rasp the shallow groove that is necessary for their successful attachment (HUGHES, 1978a, 1978b). Settlement only occurs on the surface of colonies or on patches of *Lithothamnion*-type calcareous algae that occur both on rocks and among the shells of established colonies. Long distance dispersal would therefore seem relatively unimportant. However, *D. corallinaceum* has a wide geographical range within which suitable rock faces are often separated by large tracts of unsuitable coastline. Occasional long distance dispersal in water currents must take place and an adequate mechanism for it is provided by the mucous "drogue."

Serpulorbis natalensis forms loose colonies that never monopolise space on the substratum but grow among a large variety of other sedentary organisms. The undersur-

faces and sides of stones and boulders no doubt provide a microenvironment that is less stable than the wave-swept rock faces colonised by *Dendropoma corallinaceum*. Periods of very rough weather, subtle changes in prevailing water currents and deposition of silt, or the encroachment of other sedentary organisms are factors that might cause unpredictable fluctuations in the microenvironment. Competitive ability (for space) can be increased either by forming dense colonies where individuals benefit from the anti-fouling activities of their neighbours (*D. corallinaceum*) or by remaining separate from neighbours but growing to a larger individual size (*S. natalensis*). The dense colonial structure works well in a stable habitat and where microenvironmental quality remains the same over large patches of substratum. In more unstable habitats or on more heterogeneous surfaces, *e. g.*, where microenvironmental quality changes from boulder to boulder or even within boulders, it would be better to have more widely dispersing offspring. The more isolated individuals would then have to depend on size rather than coloniality in the competition for space with other organisms. Larger size allows greater fecundity, which itself would compensate for the greater mortality accompanying wider dispersal.

SUMMARY

Newly hatched *Dendropoma corallinaceum* weighed about 37 μg total dry weight (including protoconch) of which 35.5% was protein, 1% was carbohydrate and 7.4% was lipid, suggesting that lipid was an important energy source during the dispersal phase. At 15.5°C (ambient sea temperature) the crawling young used 0.11 $\mu\text{L O}_2 \text{ h}^{-1}$ so that the energy reserves would last 4-5 days. Newly hatched *Serpulorbis natalensis* weighed about 126 μg total dry weight with a biochemical composition fairly similar to that of *D. corallinaceum*. At 15.5°C the crawling young used 0.07 $\mu\text{L O}_2 \text{ h}^{-1}$ so that the energy reserves would last 18-19 days.

Dendropoma corallinaceum respired and crawled at twice the rate for a similar sized *Serpulorbis natalensis*; however, the potential maximum distance crawled prior to settlement may be much greater for *S. natalensis*, which has larger energy reserves. The majority of juveniles of both species probably disperse by crawling and settle near

the parents, but a few may undergo long distance dispersal buoyed up by using water currents and a mucous thread.

Dendropoma corallinaceum is a "K-selected" species adapted for high competitive ability in a temporally and spatially predictable environment. Accordingly it produces relatively few, large young over a protracted breeding season. *Serpulorbis natalensis* is a more fecund, wider dispersing species adapted to a more heterogeneous and perhaps less stable environment.

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Rearing Experiments on the California Market Squid

Loligo opalescens Berry, 1911

BY

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(1 Plate; 1 Text figure)

INTRODUCTION

LOLIGINID squids are important as sources of the giant axon for neurophysiological study (ROSENBERG, 1973) and as fisheries resources (VOSS, 1973). Efforts to provide a supply of squids of the genus *Loligo* by rearing them from eggs have been unsuccessful (ARNOLD, SUMMERS, GILBERT, MANALIS, DAW & LASEK, 1974; CHANLEY, 1976). HURLEY (1976) succeeded in rearing *Loligo opalescens* to 13 mm mantle length (ML) with *Artemia salina* as the primary food. *Loligo opalescens* is large at the time of hatching (Figure 1, top) and presumably is easier to rear than the considerably smaller hatchlings of *Loligo pealei* (Lesueur, 1821) and *L. (Doryteuthis) plei* (Blainville, 1823). As part of our investigations on the rearing and maintenance of loliginid squids we were able to rear *L. opalescens* to a mantle length of 17.3 mm principally on a diet of copepods.

This paper summarizes our experience in rearing *Loligo opalescens* and describes the closed-system seawater aquaria, food sources and feeding behavior, growth, and causes of mortality.

MATERIALS AND METHODS

The closed recirculating system consisted of two 64 liter capacity rectangular glass aquaria positioned side by side in a refrigerated water bath. One aquarium was the rearing tank while the other served exclusively as a filter to

maintain water quality. The filtering tank contained an oyster shell filter bed with a well-established bacterial flora to oxidize nitrogenous wastes. Two auxiliary filters, each containing polyester fiber and activated charcoal, removed particulate debris and dissolved organic substances. Sea water was air-lifted at a rate of 1 to 2 L/min into one end of the rearing aquarium and at the other end it was returned to the filtering tank by siphon. A plankton net partition (105 μ m mesh) completely separated the drain siphon from the remainder of the rearing aquarium and prevented the squid hatchlings and food organisms from being sucked into the filtering tank. This obstacle-free configuration allowed a slow, even flow of water through the rearing aquarium. Dead food and debris were removed from the rearing tank twice a day, and approximately 3% of the water volume was replaced daily with filtered sea water. An illumination cycle of approximately 12 hours light and 12 hours dark was established with fluorescent light (Westinghouse F96T12 white). Temperature was maintained between 15.0° and 17.0°C, salinity ranged from 34 to 36‰, and pH ranged from 7.91 to 8.00. We made observations from a position above the rearing tank several times a day, particularly during feeding. Total lengths (TL) of food organisms and mantle lengths of squids were measured and recorded. To avoid damage to hatchlings we measured only freshly dead squids. Using the dead specimens, we calculated a mean growth rate for each animal by dividing the total increase in mantle length by the number of days alive.

Squid eggs were collected on 15 November 1976 at a depth of 20 m from Monterey Bay, California and were

Explanation of Figure 1

Top: Ventral view of the hatchlings of *Loligo (Doryteuthis) plei* (A) and *Loligo opalescens* (B). Despite similar adult size, there is a disparity in hatchling size. Bottom: Typical swimming orientation

of a 76 day old *Loligo opalescens*. Arrows indicate fin damage that impaired swimming and was a principal cause of mortality during later stages of the experiment





transferred to Galveston, Texas via air (15 hrs) in plastic bags filled with sea water and oxygen. Four experiments were conducted using different foods. Squid hatchlings in Experiments #1 and #2 were fed brine shrimp nauplii (*Artemia salina*) exclusively. Wild copepods of various sizes, brine shrimp nauplii and adults, barnacle nauplii, larval fishes, and hatchlings of *Loligo (Doryteuthis) plei* were used in Experiments #3 and #4. The density of food organisms (mainly copepods and *Artemia*) present in the rearing aquarium on any given day did not exceed 1 organism/mL.

RESULTS

No squids survived longer than 10 days in Experiment #1 (80 hatchlings) and #2 (90 hatchlings), while 11% of the 80 hatchlings in Experiment #3 survived beyond 10 days, with one squid lasting 35 days. Of the 65 hatchlings of Experiment #4, 15% survived longer than 10 days, with 8% attaining 60 days and 1 individual lasting 79 days. The young squids in these experiments did not feed well on either nauplii or adults of *Artemia*. When fed exclusively on *Artemia*, none survived longer than 10 days. At times, the squids were seen to capture and then reject *Artemia*. On day 7 of Experiment #3, squids vigorously attacked and ate wild copepods (*Labidocera aestiva*, 2.9 to 3.5 mm TL) collected from Galveston Bay. The young squids learned to maneuver behind and above the copepods before attacking in order to avoid the long antennae, thus increasing their catching efficiency.

By far the best results were obtained in Experiment #4. The young squids in Experiment #4 initially were fed wild copepods, primarily *Labidocera aestiva*. The larger blue copepod, *Anomolocera ornata* (5.0 to 5.5 mm TL), was presented on day 19 and was readily attacked and eaten: the remains could be seen in the stomachs of the young squids. This species then became the primary food for rearing. The large transparent copepod, *Eucalanus hyalinus* (4.0 to 6.5 mm TL), was introduced as a supplemental food from day 57 to day 66. It was readily attacked and eaten. In addition to these 2 large copepods collected offshore, smaller, unidentified copepods that could not be separated out of the catch, also were eaten throughout the experiment. *Artemia* nauplii and adults were eaten at times of low availability of copepods, but the squids exhibited a clear preference for copepods. During these periods the squids searched the bottom of the tank, and on one occasion a squid was seen to grasp and eat a dead copepod even with live *Artemia* present. When we added a new supply of copepods, vigo-

rous feeding ensued. Nauplii of barnacles *Balanus* spp. (0.2 to 0.5 mm TL) were offered to the squids on days 26 to 32, but no feeding was observed. Two squids attacked but could not subdue an unidentified larval fish 1½

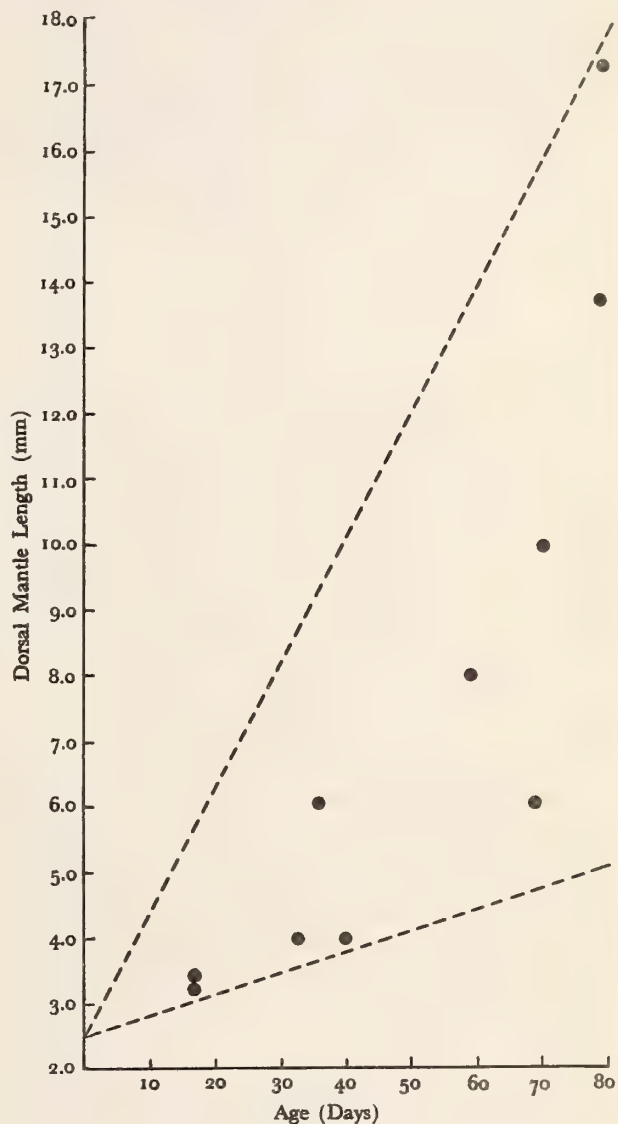


Figure 2

Age and mantle length of 10 young *Loligo opalescens* raised longer than 10 days and fed a diet of copepods. The dotted lines indicate the range of growth rates of all specimens in the experiments (1.1 to 5.6 mm per month). Mean mantle length at hatching was 2.5 mm

times their size on day 53. Subsequently (day 58), the squids ate 2 juvenile guppies (*Poecilia* sp. between 5 and 8 mm TL); however, their interest in them was slight compared to their appetite for copepods. Newly hatched *Loligo* (*Doryteuthis*) *plei* were introduced as food on day 66; the young *Loligo opalescens* appeared interested but out of 50 observed attacks, 48 were unsuccessful and only 2 hatchlings were captured and eaten.

Figure 2 presents the growth data obtained from Experiments #3 and #4 in which copepods were the main food source. The largest squid lived 79 days and measured 17.3 mm ML. Growth rates of individual squids ranged between 1.1 and 5.6 mm ML/month. In general, older animals grew faster, and the lower growth rates were obtained from squids less than 40 days old.

DISCUSSION

Two peaks of mortality occurred: the first between 1 and 10 days, and the second between 60 and 80 days. We believe that some of the early mortality resulted from the failure of hatchlings to learn how to capture prey. Young squids commonly would attack and miss copepods 4 to 7 times before capturing one. The more successful squids avoided the copepods' sensitive antennae by maneuvering above and behind the prey before attacking. We believe that later mortality primarily was due to fin abrasion. At approximately day 50 the young squids began to congregate in corners and to bump the clear glass walls of the aquarium. The fins subsequently became abraded (Figure 1, bottom), and this impaired their ability to swim and feed. Several days before death each squid was observed motionless on the bottom or swimming erratically, generally unable to feed; one was even successfully hand fed 2 times. HURLEY (1976) attributed late mortality to the possible dietary inadequacy of *Artemia*. We believe that the copepods in our experiments provided an adequate diet; however, our supply fluctuated and lower concentrations may have contributed to the late mortality.

Various foods have been fed to *Loligo opalescens* hatchlings. FIELDS (1965) observed no feeding on brine shrimp, newly hatched copepods (*Tigriopus fulvus*), algae or diatoms; no hatchling survived longer than 10 days and death was attributed to fungal infection. HURLEY (1976) reported that hatchlings fed upon brine shrimp nauplii and adults (0.7 to 5 mm TL), copepods (1 mm TL), and larval fishes (4 mm TL). She also noted that McGowan (personal communication, 1976) observed successful attacks on the mysid *Metamysidopsis elongata*. It is noteworthy that BOLETZKY (1974) reared *Loligo vulgaris* La-

marck, 1789 (2 to 3 mm TL at hatching) to 75 days on the mysid *Leptomysis mediterranea* with telsons removed to slow their escape. In general, young loliginid squids seem to prefer crustaceans and larval fishes that approximate or exceed their own size. Based upon our results and those of HURLEY (*op. cit.*) it appears that *Artemia* is an acceptable, though not preferred food. Despite large fluctuations in copepod availability during our experiments, there are indications that growth on a copepod diet was better than with an *Artemia* diet. The last surviving hatchling was 17.3 mm ML at 79 days, while HURLEY's (1976) largest hatchling was 13 mm ML at 75 days: HURLEY's (*op. cit.*: figure 3) mean hatchling size at 82 days was approximately 8 mm ML and one hatchling (8 mm ML) survived 100 days. The range of individual growth rates during our experiments (1.1 to 5.6 mm ML/month, Figure 2) was slightly higher than the 0.5 to 4.5 mm ML/month rates reported by HURLEY (*op. cit.*). From trawl data on *Loligo opalescens* reported by FIELDS (1965: 78; fig. 52), we calculated a mean growth rate of 7 mm/month for the first 3 months post-hatching. For reared squids, only the maximal individual growth rates reported by HURLEY (*op. cit.*) and ourselves compare favorably with the estimated value for wild squids.

We suggest that future experiments be conducted in round, large-volume, opaque tanks with adequate water filtration and replenishment. Emphasis must be placed upon providing a constant supply of live crustaceans such as copepods or mysids of a wide size range, perhaps reared in parallel with the squids. Collecting wild food organisms is a time-consuming, costly, and unreliable method, and can be a major limiting factor in squid rearing experiments. In all successful rearing attempts on *Loligo* species thus far, significant mortality occurred at 60 to 80 days. Apart from fin damage, this mortality peak may indicate changing food requirements at this time. We noted in a separate experiment that young, wild-caught *Loligo* (*Doryteuthis*) *plei* (12 to 22 mm ML) fed aggressively on reared post-larval white shrimp *Penaeus setiferus*, 15 mm TL. Thus, we suggest that post-larval penaeid shrimp and larval fishes may be suitable foods for *Loligo opalescens* older than 60 days.

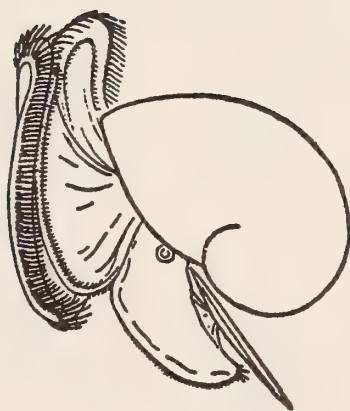
ACKNOWLEDGMENTS

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Reproductive Biology of *Colus stimpsoni* - III

(Prosobranchia : Buccinidae)

Female Genital System¹

BY

DAVID L. WEST²

(1 Plate; 6 Text figures)

INTRODUCTION

THE ORDER NEOGASTROPODA is considered to contain the most advanced prosobranchs, and all its members have internal fertilization (HYMAN, 1967; FRETTER & GRAHAM, 1962). These gastropods deposit their eggs within a resistant egg capsule which is attached in clusters or singly to various substrata. Generally, neogastropods deposit many eggs within an individual capsule; whereas, in the majority of other prosobranchs each egg is deposited in an encasing shell, along with its supply of nutrient albumin. Also, many neogastropods, in which the development has been studied, exhibit suppression of a free living larval stage, and the young emerge as miniature adults. In those species which exhibit direct development, many hundreds of eggs are deposited within a single capsule, but only a few develop. The remaining undeveloped eggs ("nutritive eggs" or "nurse eggs") serve as food for the young (THORSON, 1935, 1940; RADWIN & CHAMBERLIN, 1973; MOORE & SANDER, 1978; LYONS & SPIGHT, 1973).

With the habits of depositing numerous eggs within a capsule and of internal fertilization, the female genital system has evolved and specialized in accordance with these behaviors (FRETTER, 1941, 1946, 1953). Since fertilization must occur before nutritive and capsule forming materials are secreted around the eggs, spermatozoa must be transferred or deposited into the region of the oviduct preceding the secretory areas. However, spermatozoa are generally deposited at the terminal end of the female duct. Spermatozoa may be stored at the terminal end, within the bursa copulatrix, or they may be passed up the oviduct and stored within specialized regions connected to the gonoduct, such as the seminal receptacle or the ingesting gland (FRETTER, 1941, 1953; HOUSTON, 1976).

Organization of the female neogastropod genital system appears to be rather uniform throughout the order (PONDER, 1974; HOUSTON, 1976; SMITH, 1967; FRETTER, 1941, 1946), with differences in the location of the seminal receptacle, ingesting gland and bursa copulatrix, or in the presence or absence of some of these structures. The female system generally consists of a single tube extending from the ovary, along the visceral mass, into the mantle cavity where it passes along the roof. In lower gastropods, the ovary is connected to the right nephridium, and the gametes are discharged into the water via the nephridiopore. However, in neogastropods the ovary opens into the mantle region by a duct. Various terms, some indicating a functional relation, others having phylogenetic implications, have been applied to the duct extending along the visceral mass. However, in the present study, the term "renal oviduct" will be used to denote that portion of the oviduct extending along the visceral mass, and "pallial oviduct" for that portion extending along the mantle roof. The genital ducts of the muricid *Thais* (*Nucella*) *lapillus* (Linnaeus, 1758) and the buccinid *Buccinum undatum* Linnaeus, 1758, are frequently used as examples of neogastropod reproductive systems and are considered typical of this order (HYMAN, 1967; FRETTER & GRAHAM, 1962; PONDER, 1974). However, many members of the Buccinidae have not been investigated. The present study concerns the female reproductive system of the buccinid *Colus stimpsoni* (Mörch, 1867) to further the knowledge of its phylogenetic relationships and its relation to the reproductive strategy of direct development and nutritive eggs.

MATERIALS AND METHODS

Snails of various sizes were collected intertidally at Cobscook State Park, Edmunds, Maine, and at Eastport, Maine, and maintained in running sea water aquaria (WEST, 1973, 1978). To determine the sex of individual

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snails, the animals were placed on a dry table with the body aperture facing upward. After a few minutes the snails would try to right themselves. During this period, the presence or absence of a penis could be noted as the foot extended over the edge of the shell. Snails were segregated according to sex, measured, and an identifying number affixed to the shell.

For histological studies, tissues were excised from freshly opened snails and processed according to the methods described in the first paper of this series (WEST, 1978).

RESULTS

General Morphology

The ovary, a deep orange-brown to orange-yellow in color, lies on the distal-most portion of the visceral mass in the ultimate and in part of the penultimate whorls of the shell (Figure 1). The ovary and visceral mass are covered by a single layer of cuboidal epithelium, the pallial epithelium, and a thin layer (20-60 μm thick) of connective tissue and muscle. In large females (80mm or greater in shell length), the ovary may cover more than one-half of the digestive gland.

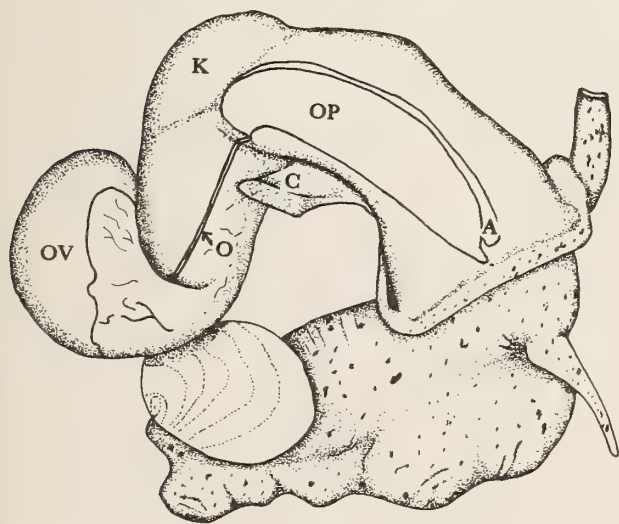


Figure 1

Female *Colus stimpsoni*: whole animal with shell removed and the mantle drawn as transparent: A - anus; C - columellar muscle; D - digestive gland; K - kidney; OV - ovary; OP - pallial oviduct; O - renal oviduct

The oviduct emerges from the ovary and passes as a single straight duct along the columellar side of the visceral mass beneath the pallial epithelium. At the posterior limits of the mantle cavity, the oviduct turns abruptly dorsad and enlarges. The enlarged portion reflexes anteriorly and continues in the mantle roof, alongside the rectum. The oviduct consists of 2 morphologically distinct portions, a thin-walled renal oviduct which passes along the visceral mass, and a glandular, pallial oviduct which passes along the mantle (Figure 1). The pallial oviduct is opaque white in color and is the most noticeable portion of the genital duct in gross dissection. The pallial oviduct narrows at its anterior end forming a short vagina. In sexually mature females, the pallial oviduct varies from 3 to 6 cm in length and is oval in cross section, measuring 5 to 18 mm in long axis and 3 to 9 mm in short axis.

Near the junction of the renal and pallial oviducts, at the posterior end of the mantle cavity, a small duct, the gonopericardial duct, opens into the renal oviduct. The gonopericardial duct (Figure 2) passes posteroventrally toward the pericardium. However, this duct could only be traced to within a very short distance from the pericardium.

Histology

Ovary: The ovary is a multitubular organ with the tubules generally oriented perpendicular to the spiral axis of the shell. The ovary is separated from the digestive gland, but ovarian tubes occasionally intrude between the tubules of the digestive gland. Ovarian tubules are separated from one another by a layer (2-8 μm in thickness) of loose connective tissue and muscle fibers. Beneath this layer is a basal lamina which varies from 0.1-0.3 μm in thickness and is composed of a dense layer of fibers. Young oocytes and follicle cells lie on the periphery of the tubule subjacent to the basal lamina. Vitellogenic and postvitellogenic phases of oocyte development occur in the center of the tubule. The ovarian tubules eventually join to form the single oviduct.

Renal Oviduct: The thin-walled renal oviduct is embedded in loose connective tissue and varies from 500 to 800 μm in diameter (Figure 3). The wall (10 to 20 μm thick) is composed of circular muscle and connective tissue. The duct is lined with a simple columnar epithelium which rests on an indistinct basal lamina. Epithelial cells vary in height with tall cuneiform cells projecting into the lumen at irregular intervals. These tall cells (75-100 μm in height) are surrounded by decreasingly shorter cells

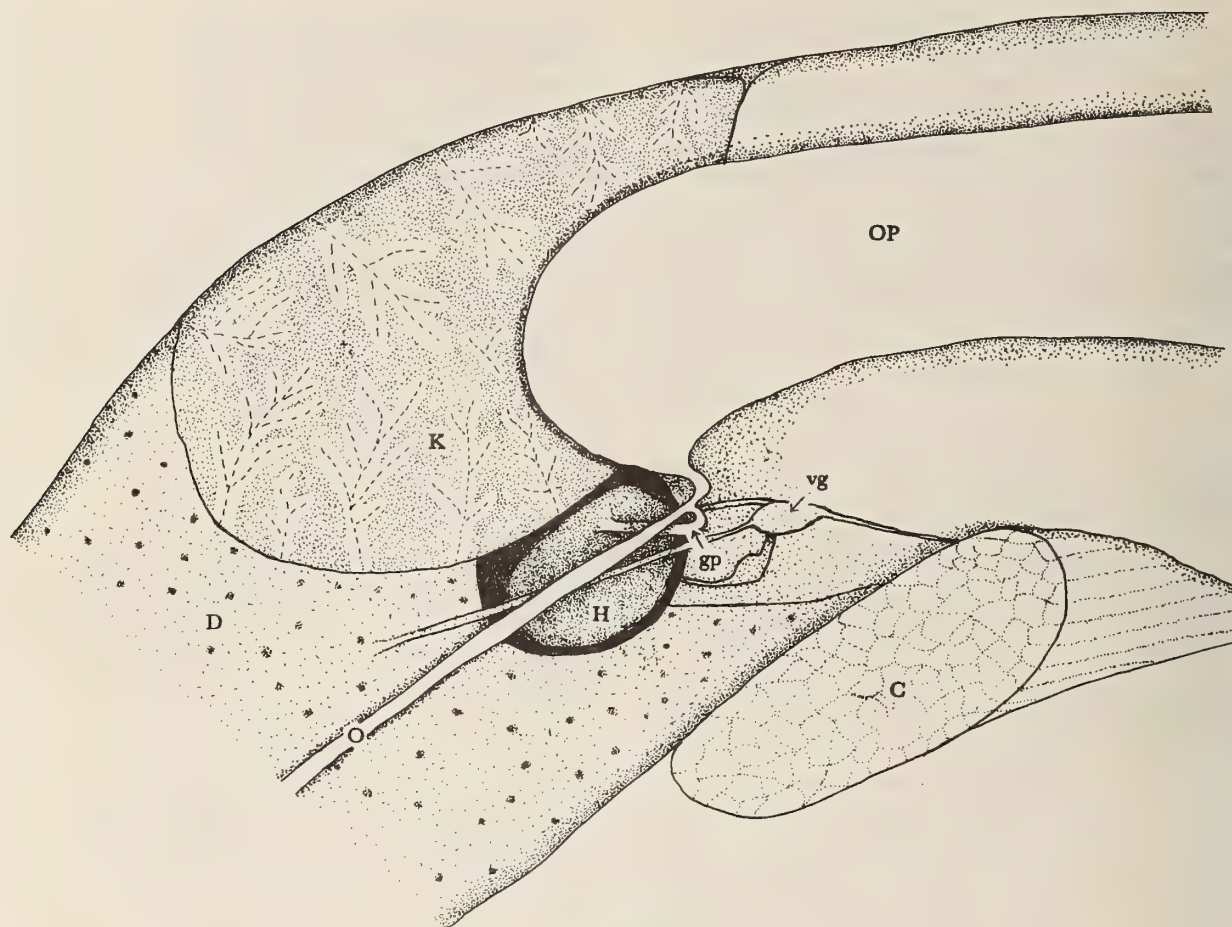


Figure 2

Drawing of gonopericardial duct and its relation to the genital duct: C - columellar muscle; D - digestive gland; GP - gonopericar-

dial duct; H - heart; K - kidney; OP - pallial oviduct; O - renal oviduct; VG - visceral ganglion. (Not drawn to scale)

with the shortest cells measuring $25-30\mu\text{m}$ in height. The variation in cell height gives the epithelium a mucosa-like appearance. Nuclei of the epithelial cells are irregular in outline and vary from $7-12\mu\text{m}$ in length. Occasionally, within the renal oviduct, disrupted oocytes are observed, and the surrounding epithelial cells contain yolk platelets.

Pallial Oviduct: The renal oviduct turns sharply dorsad near the posterior limits of the mantle cavity and becomes glandular, forming the pallial oviduct. The pallial oviduct is composed of 3 parts: a glandular region, a bursa copulatrix, and the vagina. These components of the oviduct are surrounded by a layer of connective tissue and muscle giving the appearance of a single enlarged tube.

Explanation of Figures 6 to 8, 10 and 11

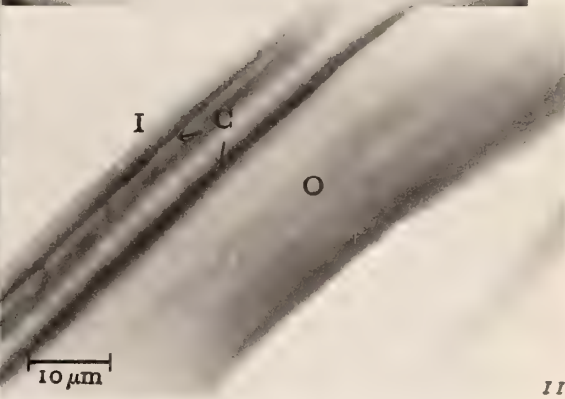
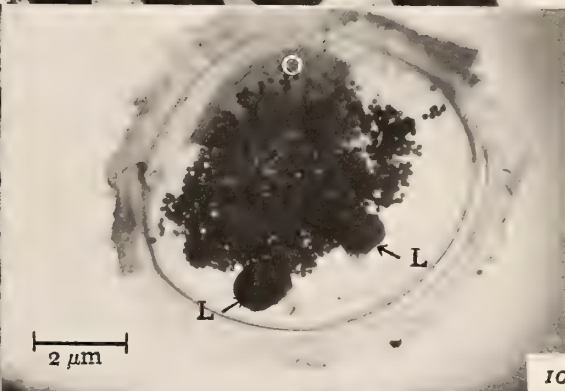
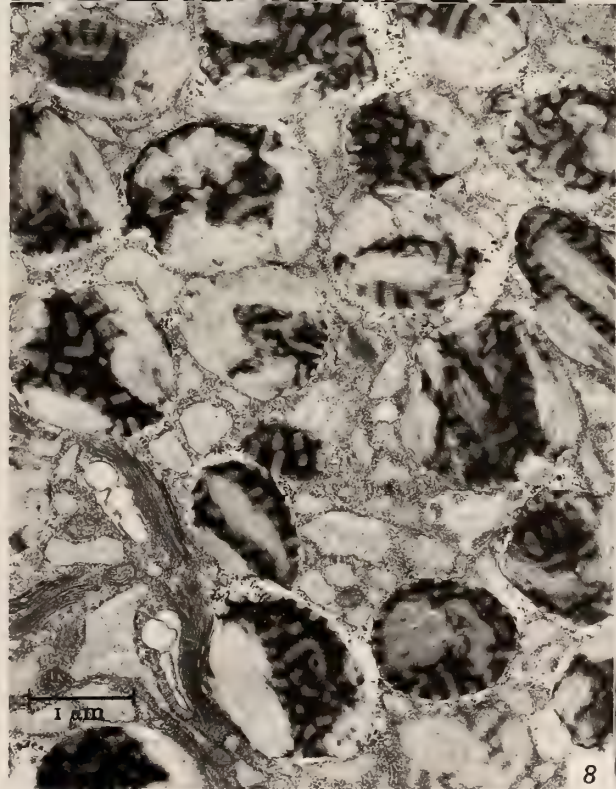
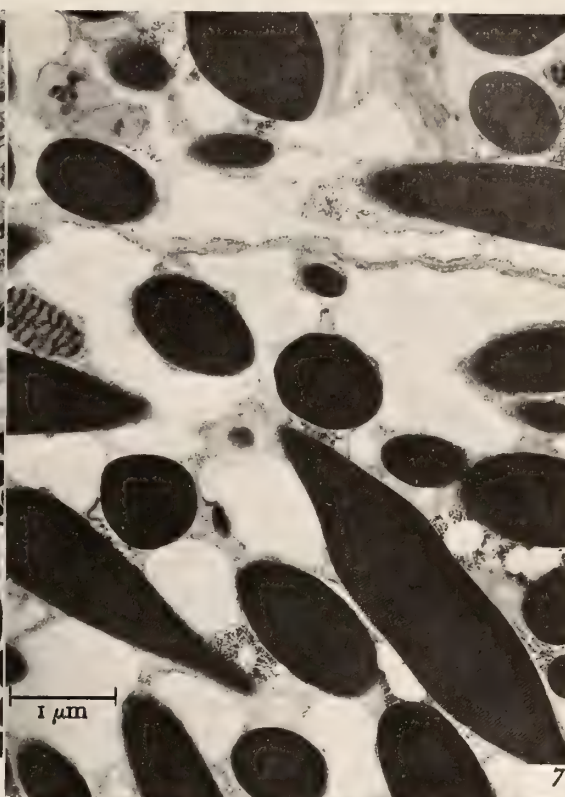
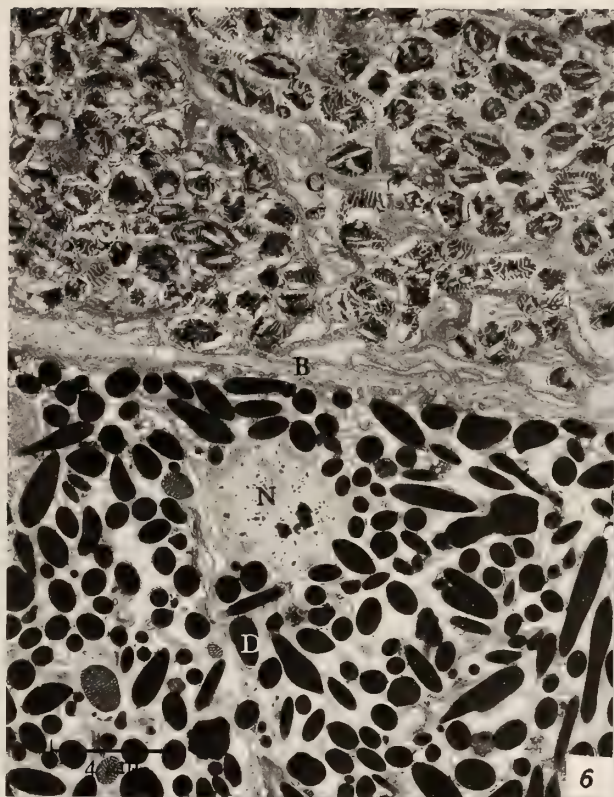
Figure 6: Electron micrograph of capsule gland wall showing the dorsal differential-staining region (D) and the central region (C): B - basal lamina and connective tissue between tubules; N - nucleus

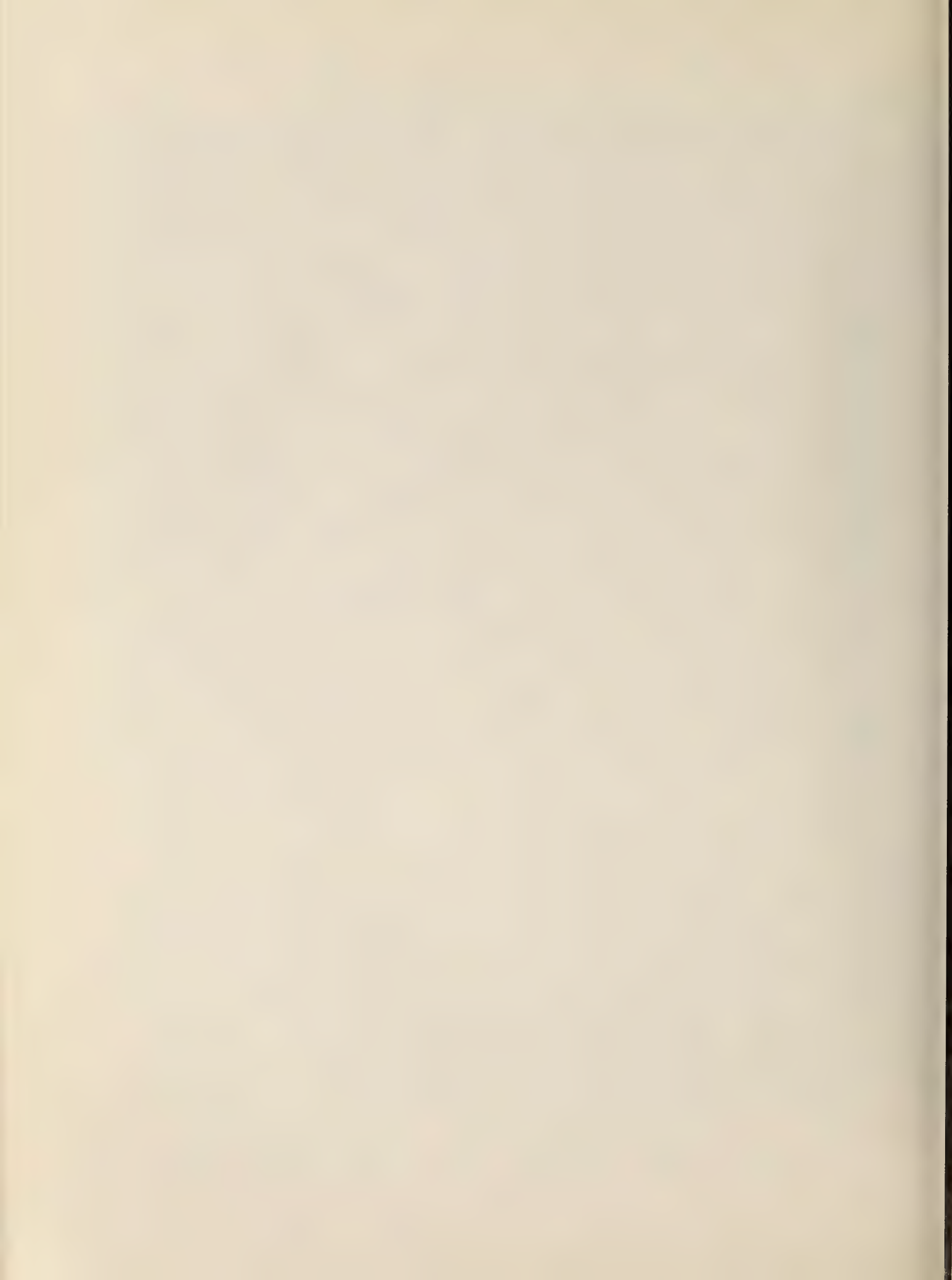
Figure 7: Electron micrograph of gland cell granules within dorsal and ventral differential-staining regions of the capsule gland

Figure 8: Electron micrograph of the gland cell granules within the central region of the capsule gland

Figure 10: Egg capsule of *Colus stimpsoni*: L - larva; O - capsule operculum

Figure 11: Light micrograph of egg capsule wall: C - central layer; I - inner layer; O - outer layer





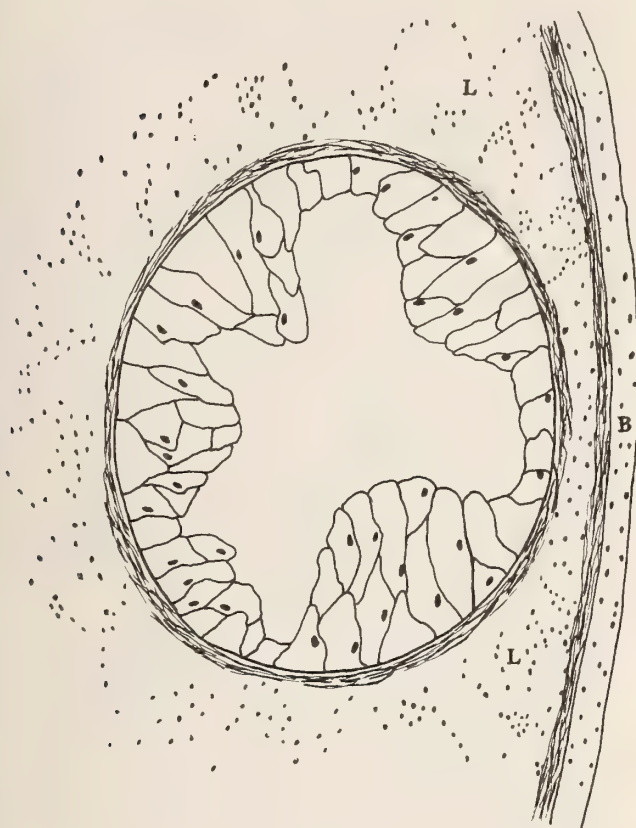


Figure 3

Line drawing of a cross section through renal oviduct: B - body wall; L - loose connective tissue

Slightly posterior to the transition region between the pallial and visceral portions, the oviduct reflexes sharply posteriad and passes out of the mantle into the body between the kidney and body wall. This portion is parallel and dorsal to the renal oviduct. At a point about $\frac{1}{3}$ along the kidney, the oviduct turns abruptly forward and passes back into the mantle. These turns form an S-shaped loop. This loop is covered by the connective tissue surrounding the pallial oviduct and is not visible in gross dissections, as shown in Figure 2.

The glandular segment constitutes the largest part of the pallial oviduct and is histologically similar along its length but has differentially staining regions. The posterior end (5 - 10 mm in length) corresponds to the albumin gland reported in other neogastropods and the remaining glandular area corresponds to the capsule gland (FRET-

TER, 1941; HOUSTON, 1976). In cross section, the albumin and capsule glands are composed of right and left lobes. These lobes are connected dorsally and ventrally by relatively thin walls which give the lumen of the oviduct the appearance of a dorso-ventral slit (Figure 4).

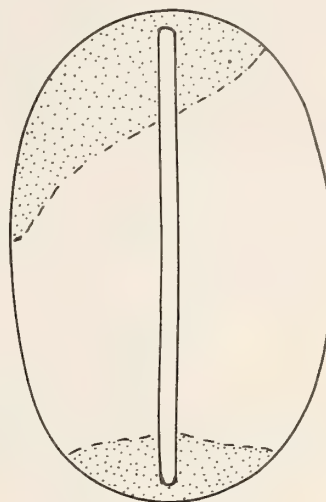


Figure 4

Line drawing of a cross section through the capsule gland; stippled areas show extent of dorsal and ventral differential-staining regions

The epithelium of the pallial oviduct consists of tall, ciliated columnar cells (20 - 40 μ m in height), which have elongated, ellipsoidal nuclei, and numerous gland cells (Figure 5). The gland cells are tightly packed together, forming rod-shaped or tubular glands which are elongated and coiled distally. These glands are packed together, and each is enclosed by the basal lamina of the epithelium (Figure 6). Gland cells are large with subspherical, basally located nuclei. These cells are elongated, and the necks of the cells extend to the surface through the center of the gland (Figure 5). The glands have no lumen *per se*, but rather a core of cell necks which are filled with secretory granules. While the distal cells of a gland have much longer necks than do the proximal ones, there is no apparent difference in the diameter. Glands along the dorsal and ventral walls of the oviduct are shorter in length (0.3 - 0.5 mm vs. 1.5 mm) than ones along the lateral walls (see Figure 4). Blood lacunae are irregularly distributed throughout the walls of the pallial oviduct and

appear as numerous, small spaces in sectioned material (Figure 5).

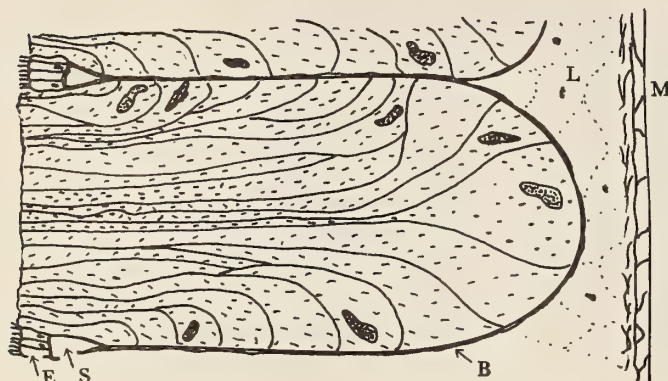


Figure 5

Line drawing of capsule gland wall showing tubule glands: B - basal lamina; M - mantle cavity; E - ciliated cells of epithelium; L - loose connective tissue; S - blood sinus. (Not drawn to scale)

The albumin and capsule glands stain differentially from one another with the azo-carmin procedure. The granules of the albumin gland cells stain predominantly pale blue; whereas, those of the capsule gland cells stain predominantly purple and pale violet. The albumin gland gives rise to the capsule gland at a region opposite the posterior end of the ctenidium. Near this area, the right dorsolateral wall of the albumin gland forms a fold of glandular tissue. This fold extends ventrally into the lumen and is attached to the ventral wall at the apex of the fold. This fold is about 5 mm in length and is covered laterally with a ciliated epithelium. The fold extends into the posterior limits of the capsule gland and divides the lumen into right and left portions.

The capsule gland walls are thicker than the albumin gland walls and have differentially staining areas within them. In cross section, the dorsal $\frac{1}{3}$ and ventral $\frac{1}{3}$ stain predominantly red to purple and the middle section stains predominantly blue to pale violet with the azo-carmin stain (Figure 4). The middle section also stains deep blue-black with Heidenhain's hematoxylin. Within these regions of the capsule gland, the gland cells contain both red and blue staining granules. However, these regions are dominated by one staining type of granule. The granules of the gland cells in the dorsal and ventral portions are predominantly fusiform to rod-shaped (Figure 7);

whereas, the granules of the central portion are spherical (Figure 8).

The cytoplasm of the cells of the dorsal and ventral portions of the capsule gland is dominated by numerous vacuoles which contain flocculent material, in addition to the dense granules (Figure 7). The granules are electron-dense with alternating bands of slightly less electron densities, having a periodicity of about 250 Å (Figure 7). The cytoplasm contains a few mitochondria as well as glycogen particles and the Golgi complex. The cisternae of the Golgi complex are filled with an electron-dense material.

The granules of the gland cells within the central portion of the capsule gland are membrane-bounded and are composed of electron-dense granular material and a somewhat less electron-dense fibrous substance (Figure 8). The granular material is distributed in patches broken up by the fibrous material. Well-developed Golgi lamellae are scattered within the cytoplasm, and the cisternae contain an electron-dense granular substance. The cisternae of the rough endoplasmic reticulum are enlarged and contain dispersed granules which are about the same electron-opacity as the neighboring cytoplasm (Figure 8).

The bursa copulatrix is situated at the anterior end of the capsule gland (Figure 9). It is oval in lateral view, and the capsule gland slopes ventrally beneath it. The lumen of the oviduct passes beneath the bursa copulatrix, opening into the vagina, and the ciliated columnar epithelium (20 - 50 μ m thick) of the oviduct is folded in this region. The bursa copulatrix is a muscular chamber and is separated from the capsule gland and the wall of the oviduct beneath it by a layer of loose connective tissue and muscle. The wall of the bursa measures 200 - 500 μ m in thickness, and the epithelium is ciliated and folded. The duct connecting the bursa copulatrix and vagina is histologically similar to the bursa and is separated from the wall of the oviduct by a layer of loose connective tissue. Sperm fill the bursa copulatrix and its duct throughout the year. Around the periphery of the bursa, the heads of the sperm are oriented toward the epithelium and are in contact with it. The duct of the bursa copulatrix opens into the vagina a short distance from the female opening. The vagina is lined with columnar and mucous-secreting cells. Beneath this epithelium is a layer of muscle and connective tissue. The vagina is 5 - 10 mm in length and closed by a sphincter (Figure 9).

Cytochemistry of Pallial Oviduct

Results obtained from sections embedded in polyester wax and stained with Lehmann's polychrome indicate a num-

ber of macromolecular groups are present in the pallial oviduct. The different regions of the capsule gland contain both protein and mucopolysaccharides, and the albumin gland is rich in mucopolysaccharides. The dorsal and ventral portions of the capsule gland are dominated by the presence of an acid or neutral protein. The central portion is dominated by mucopolysaccharides, probably acid in nature. Table 1 records the results of the specific cytochemical tests.

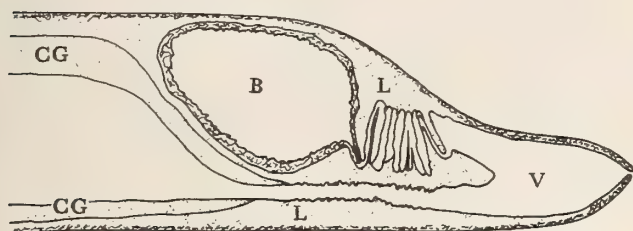


Figure 9

Line drawing of a longitudinal section through posterior portion of the pallial oviduct: B - Bursa copulatrix; CG - capsule gland wall; L - loose connective tissue; V - vagina. (Not drawn to scale)

Table 1

Results of specific cytochemical tests of the pallial oviduct of *Colus stimpsoni*

Technique	Albumin gland	Capsule gland		
		Dorsal	Ventral	Central
PAS	+	+	+	+++
Alcian Blue (1.0)	-	+	+	+++
Alcian Blue (2.3)	-	+	+	+++
Bromphenol Blue	++	+++	+++	+

+, ++, +++, increasing degrees of positive staining intensity; -, negative reaction

Spawning

Females deposit egg capsules throughout the year with increased deposition from February to May. Eggs are passed down the oviduct to the albumin gland, where sperm incorporation apparently occurs. During one dissection, motile sperm were recovered from the posterior part of the albumin gland. The eggs are moved down the pallial oviduct, and secretions from the albumin and capsule glands accumulate around the eggs. This mass is

passed from the female opening to the edge of the foot, and subsequently moved to the pedal gland located in the midline of the foot about $\frac{1}{3}$ of the way back from its anterior edge. This behavior is very similar to that of *Melongenacora corona* (Gmelin, 1791) described by BINGHAM & ALBERTSON (1973). The pedal gland shapes the egg capsule, and the female presses the capsule against the substratum with the foot, maintaining this position for from 5 - 12 hours. Capsules are deposited singly and are attached to various hard substrata.

In surface view, the capsules are circular to oval (10 to 16mm in diameter) and, in side view, are subhemispherical to hemispherical, measuring 4 - 8mm in height. The opaque, white capsule operculum is fusiform to oval in shape and measures 4 - 5 mm in long axis and 3 - 4 mm in short axis. When the capsule is viewed from the side, the operculum is situated about in the middle of the capsule. Capsules are whitish with a yellow central portion containing the eggs which are suspended in a viscous albuminous fluid (Figure 10).

The capsule wall (Figure 11) is composed of 3 differentially staining layers. The innermost layer (5 - 10 μ m thick) stains light blue with the azo-carmin technique and is composed of fine fibers. The fibers are oriented circularly around the egg mass. The central layer (5 - 10 μ m thick) is also composed of fine fibers and stains light red with azo-carmin. The outermost layer is thicker than the other 2 layers (40 - 50 μ m thick) and is composed of a coarse, fibrous material. This layer stains light blue with the azo-carmin procedure. Occasionally sperm were observed in the albumin surrounding the eggs and also embedded in the capsule wall. The number of eggs in a capsule varies from 200 to approximately 6800. Generally, however, capsules contain between 4000 and 5500 eggs with an average of 4700. An average of 4 embryos develop in a capsule, with a range of 0 to 8.

DISCUSSION

In the female genital system of neogastropods, the thin-walled portion of the gonoduct generally passes as a single, straight duct along the visceral mass and continues as a glandular portion in the mantle. The pallial portion usually consists of an albumin gland, ingesting gland, capsule gland, bursa copulatrix, and vagina (HOUSTON, 1976; FRETTER, 1941; FRETTER & GRAHAM, 1962; PONDER, 1974). The ingesting gland ingests sperm and sometimes yolk, but in some species it functions as a seminal receptacle (FRETTER, 1941). The capsule gland is usually the largest region and has several areas showing different staining properties in histological preparations. Typically, this gland has a ventral, non-ciliated channel which is overhung by 2 or 3 ciliated folds.

In *Colus stimpsoni*, the female genital system conforms to the general conditions found in other neogastropods with a few exceptions. An ingesting gland is not present, and no region of the pallial oviduct appears to serve as a sperm-ingesting function. A seminal receptacle is also absent. The lumen of the oviduct in *C. stimpsoni* is completely ciliated, and no ventral channel is present.

The walls of the albumin and capsule glands are composed of numerous simple tubular glands. FRETTER (1941) described the walls of these glands in *Thais lapillus* as being composed of groups of cells lying at various heights, and the ducts of these groups run to the surface of the ciliated epithelium. The albumin and capsule glands in *Colus stimpsoni* appear very similar to those of *T. lapillus* according to the description and figures of FRETTER (*op. cit.*). However, these walls are composed of simple epithelial gland cells. These gland cells are clustered tightly together and drop below the surface of the ciliated epithelium but their apical ends reach to the level of the ciliated epithelium. These gland cells share the common epithelial basal lamina, and they secrete their products directly into the lumen, with no duct present.

An ingesting gland or sperm-resorbing areas have been reported in a number of neogastropods. However, HOUSTON (1976) indicates that *Colus gracilis* (da Costa, 1778) also lacks an ingesting gland, as in *C. stimpsoni*, but that a seminal receptacle is present. Special significance has been attributed to these areas (FRETTER, 1941; HOUSTON, *op. cit.*). It has been suggested that the growth of ova is dependent on sperm absorption and on materials derived from sperm breakdown. It has also been suggested that the female uses the ingesting areas to remove excess sperm (FRETTER, *op. cit.*). It appears that fertilization occurs in the albumin gland (see also HOUSTON, *op. cit.*), at the posterior end of the pallial oviduct. It is reasonable to assume that not all sperm passed to the albumin gland are utilized in fertilization, and that the moribund or dead sperm must be removed. In *C. stimpsoni*, the presence of sperm in the albumin surrounding the eggs and in the capsule wall suggests that excess sperm are voided with the egg mass, and females rid the oviduct of excess sperm by passing them out of the oviduct with the spawn mass.

Seminal receptacles generally occur in neogastropods and are located between the albumin and capsule glands. Following copulation, sperm are transferred along the ventral channel of the pallial oviduct to the seminal receptacle, where they are stored. The seminal receptacle may be divided, and one portion serves as an ingesting gland. In *Colus stimpsoni* no indication of an ingesting gland or seminal receptacle was observed. Also, a ventral channel is absent. In *C. stimpsoni*, the function of sperm storage appears to involve only the bursa copulatrix, and perhaps sperm are only transferred to the albumin gland

during spawning periods. The absence of both a seminal receptacle and ingesting gland in *C. stimpsoni* is consistent with the suggestions of FRETTER (1941) and HOUSTON (1976) that these structures may have a common origin and are homologous.

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Egg Capsule and Young of the Gastropod *Beringius beringii* (Middendorff) (Neptuneidae)

BY

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(1 Plate)

INTRODUCTION

THE PROSOBRANCH GASTROPOD, *Beringius beringii* (Middendorff, 1849) reportedly ranges from the Shumagin Islands, off the south side of the Alaska Peninsula, north to Point Barrow and the Amundsen Gulf in the Canadian Arctic (MACPHERSON, 1971). Recent trawl surveys conducted by the National Marine Fisheries Service have shown *B. beringii* to be common at depths between 53 and 163 m on the eastern Bering Sea shelf (PEREYRA *et al.*, 1976: 345).

The egg capsule and young of *Beringius beringii* collected in the eastern Bering Sea are described in this paper. Although several species of *Beringius* occur in the northeastern Pacific Ocean and eastern Bering Sea, only the egg capsule and young of *B. eyerdami* Smith have previously been described (COWAN, 1964) from this area.

COLLECTION SITES AND METHODS

During a bottom trawl survey in the eastern Bering Sea between June 21 and July 13, 1976, 2 live *Beringius beringii* and several egg cases presumed to be those of the same species were collected. The egg cases were preserved in 10% formalin. The 2 snails, 155 and 125 mm in total length, were held aboard ship in a circulating seawater tank and, in August, placed in a saltwater aquarium and held at 5° - 6°C in Kodiak, Alaska. These snails readily consumed the meat of pink shrimp, *Pandalus borealis* Krøyer, when fed at weekly or biweekly intervals.

On April 22, 1977, the larger *Beringius* (Figure 1) laid a single capsule on the wall of the aquarium. The capsule was 39 mm high, 35 mm wide, and 7.5 mm thick (Figure 2). Its width decreased to 21 mm near its base where it then flared out, forming a flattened 16 × 30 mm surface for attachment to the substratum. The outer surface

of the capsule was pale yellow and had a smooth, untextured, rubber-like surface. The capsule was removed from the wall of the aquarium and measured, but was not examined internally.

Three rows of capsules were collected on July 11, 1976, at 57°41'N latitude, 170°16'W longitude, north of the Pribilof Islands in the eastern Bering Sea, and preserved in 10% formalin. These capsules, although similar in color, texture, and form, vary in size and relative proportions. Capsules ranged from 33 to 41 mm high and 37 to 40 mm wide. In each of the 3 rows, the capsules were laid in a straight line and one capsule generally overlapped the next (Figure 3). Two rows contained 5 capsules while the third contained 7. One row of capsules was laid on the shell of a live *Beringius beringii* and 2 rows were laid on dead *Neptunea heros* (Gray) shells. Because of the regular orientation of the capsules, it appears that a single female lays an entire row.

The capsule laid in the aquarium closely resembles those taken near the Pribilof Islands with only minor differences in size and relative proportions. Among the Pribilof capsules, slight variations in these features appear to be the rule.

THE EGG CAPSULE

As described by COWAN (1964) for *Beringius eyerdami*, each capsule was a complete envelope within an envelope (Figure 4). Each layer was about 0.15 mm in thickness. The outer surface of the capsule was smooth and rubber-like. The interior surface of the outer envelope was covered with fine ridges running parallel to the axis of the capsule base. Between the 2 envelopes was a layer of slender yellow fibers that lay parallel to these ridges. The fibers, about 30 - 35 mm long, were loosely attached to the walls of the envelopes, allowing the 2 walls to be easily separated. The outer surface of the inner envelope was also

covered with fine ridges along the same axis. The surface lining the brood chamber was, like the exterior of the capsule, smooth and rubber-like.

Of the 17 capsules examined, 13 contained embryos. The 3 separate rows of capsules contained embryos at different stages of development; however, within a row, development was quite uniform. In the first row of capsules, all but one embryo had escaped. All 5 capsules were ruptured for nearly their entire width on the ventral surface about 2 mm from the capsule's edge. The single embryo that remained in this cluster was not the largest of all those examined, but was the most distinctively marked (Figure 5). The 5 capsules of the second row each contained from 13 to 15 poorly developed embryos. The foot and mantle of these 6 mm embryos were well formed but no calcareous shell had developed. The 7 capsules in the third row contained embryos from 10 to 16 mm long that were probably close to hatching, as judged by comparison with the size and sculpturing of the previously examined embryo (Figure 5). The number of embryos per capsule ranged from 1 to 6 and was inversely proportional to the mean size of the embryos (Table 1).

There were significant differences in the average number of embryos per capsule in the second and third capsule rows. It is questionable that 15 embryos could all grow within a capsule to a size and condition that would insure their post-embryonic survival, although SPICHT (1976) stresses the variability in hatching size among nurse-egg feeding prosobranch gastropods. THORSON (1940) suggests that when large numbers of embryos inhabit a capsule, the embryos will leave the capsule and commence their free life on the sea bottom at a comparatively early stage of development. Data presented herein suggest that the size of the embryo at any given stage of development is greater in the less crowded capsule (Table 1). Both of these relationships may hold true for *Beringius beringii*.

THE YOUNG SNAILS

The well-developed capsule young had from 1 to 1 $\frac{3}{4}$ nuclear and $\frac{1}{2}$ to 1 $\frac{1}{2}$ post-nuclear whorls. The nucleus was generally white to pink, while the post-nuclear whorls

Table 1

Number of embryos per capsule and dimensions of well developed young in a row of seven *Beringius beringii* egg capsules.

Capsule Number	Number of embryos per capsule	Embryo length—mm		Aperture length—mm		Width of first nuclear whorl—mm		number of nuclear whorls	
		mean	range	mean	range	mean	range	mean	range
1	2 ¹	13.1	—	6.9	—	5.7	—	1 $\frac{1}{4}$	—
2	1	16.0	—	7.3	—	5.7	—	1 $\frac{1}{4}$	—
3	3	12.4	11.8-13.4	7.4	7.0-7.8	5.9	5.4-6.4	1 $\frac{1}{4}$	1 $\frac{1}{4}$ -1 $\frac{1}{2}$
4	5	11.1	10.3-11.6	7.1	6.7-7.3	5.3	4.9-5.7	1 $\frac{1}{4}$	—
5	6	10.4	10.0-10.9	6.6	6.2-6.9	5.2	4.6-5.8	1 $\frac{1}{4}$	1 $\frac{1}{4}$ -1 $\frac{1}{2}$
6	1	15.8	—	8.4	—	2	—	1 $\frac{1}{4}$	—
7	4	11.6	10.7-13.3	6.9	6.1-7.8	5.6	5.0-6.2	1 $\frac{1}{4}$	1-1 $\frac{1}{2}$
Means									
Combined		11.7		7.0		5.5		1 $\frac{1}{4}$	

¹One is crushed, no measurements obtained.

²Damaged, no measurement obtained.

Explanation of Figures 1 to 5

Figure 1: *Beringius beringii* specimen that laid egg capsule on aquarium wall

Figure 2: Egg capsule removed from aquarium wall

Figure 3: Cluster of 5 egg capsules laid on shell of *Neptunea heros*

Figure 4: Diagram showing capsule wall of *Beringius beringii* egg capsule:

a. Outer layer showing fine striations on inner surface

b. Layer of slender yellow fibers

c. Inner layer showing fine striations on outer surface

Figure 5: Juvenile *Beringius beringii* taken from open egg capsule



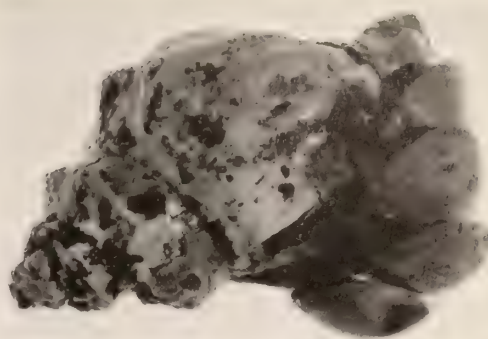
Figure 1

2 cm



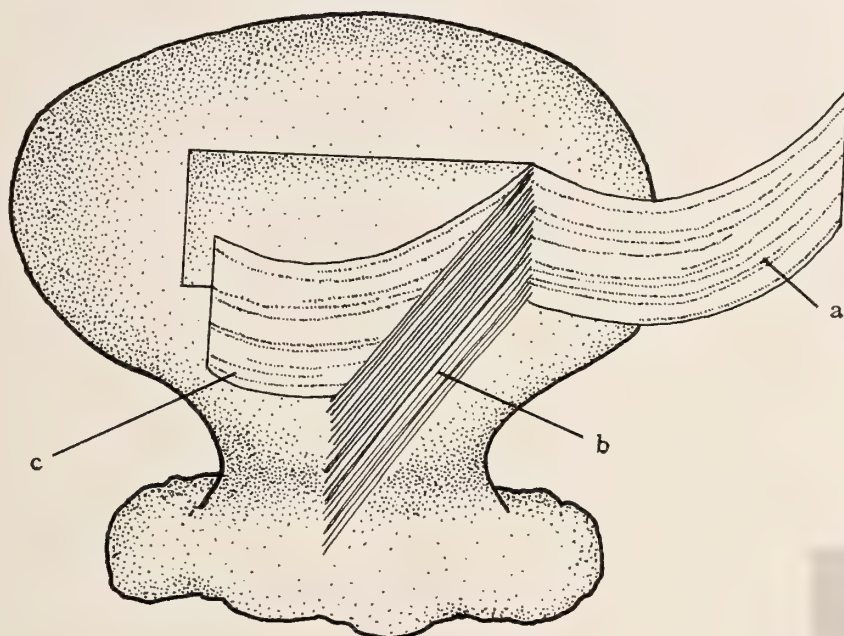
2 cm

Figure 2



2 cm

Figure 3



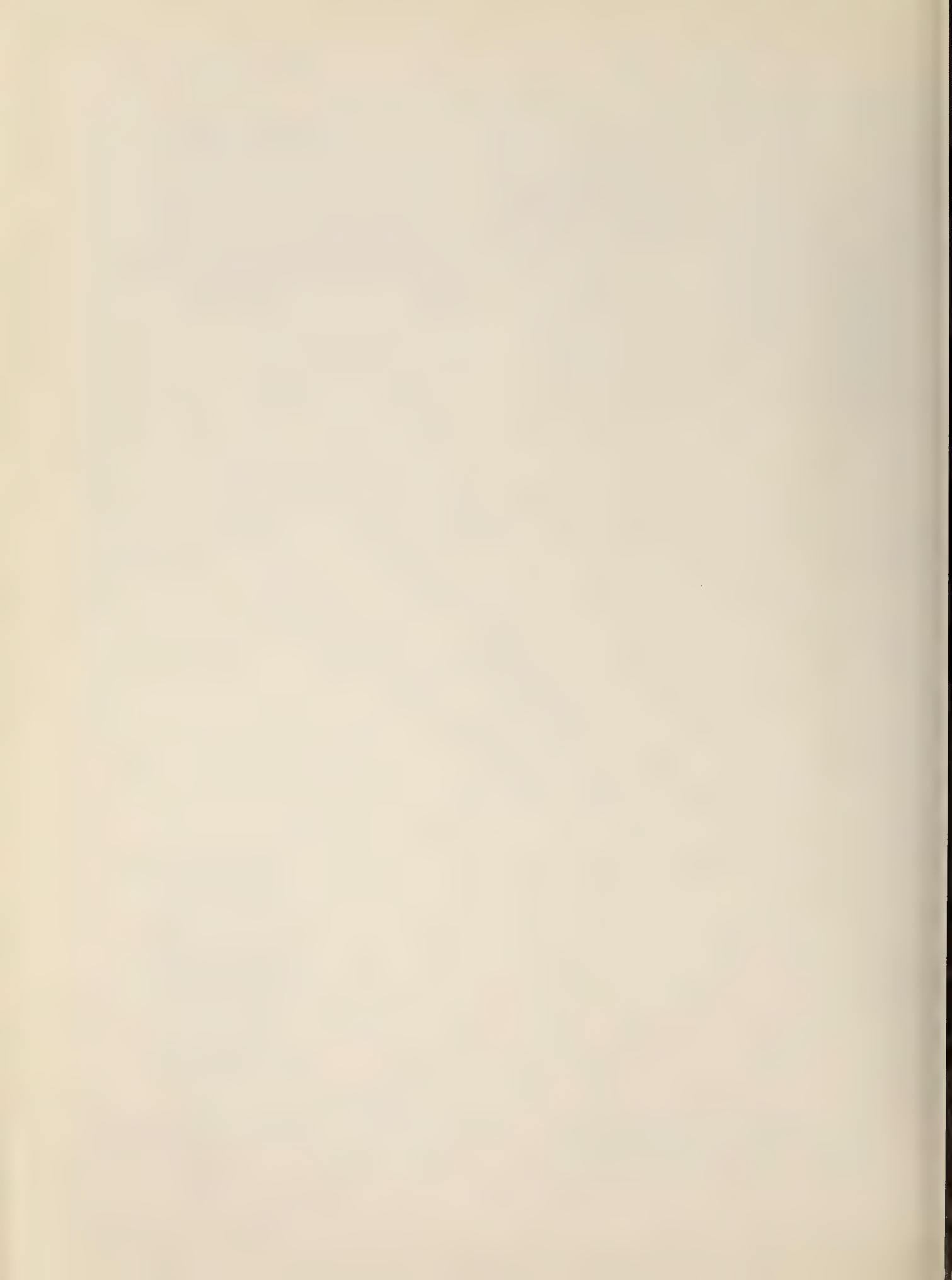
2 cm

Figure 4

5 mm



Figure 5



ranged from pink to pinkish-brown. The color change was often quite clear cut. As in *Beringius eyerdami*, the apical concretion of the first nuclear whorl was small and discrete with the sutural groove originating at nearly the center of the snail's apex. The first few millimeters of the suture were deeply channeled. Covering the nucleus was a thin parchment-like film that adhered tightly to the lower end of the nucleus, but became loosely attached and sack-like near the apex. This sack was filled with a clear fluid in some specimens and extended in a spiral pattern for about 5 mm beyond the apex. In most specimens, however, the sack was empty and appeared as a shriveled cap atop the nucleus. This sack was not present on the single embryo in the open egg case.

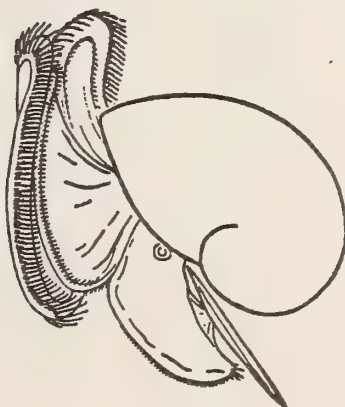
The post-nuclear whorls of capsule young closely resembled those of adults of the species. The body whorl of the capsule young was moderately inflated and the anterior canal was straight, short, and broad. Spiral sculpture consisted of 2 to 9 faint, nonparallel, and irregularly spaced threads of varying length that extended from the suture to well below the periphery. The base of the body whorl was covered with up to 16 closely spaced spiral grooves, extending from a point below the periphery of the body whorl to the end of the anterior canal. Rounded axial ribs began to appear on the second post-nuclear whorl, and the entire whorl was covered by fine incremental growth lines. Essentially, all of the shell characters that distinguish adult *Beringius beringii* were also

present in the well developed capsule young.

COWAN (1964) found that the shape and sculpture of well-developed capsule young of *Beringius eyerdami* closely resembled that of adults of the species. This similarity also exists with the capsule young and adults of *B. frielei* Dall, 1895 from the eastern Bering Sea (personal observation). The only other *Beringius* in the area that could conceivably be confused with the young of *B. beringii* is *B. stimpsoni* Gould, 1860. Adult *B. stimpsoni* have flat sided whorls and are strongly carinate, 2 features entirely absent in *B. beringii*. The embryos described herein so closely resemble adult *B. beringii* that they can reasonably be ascribed to this species.

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Abnormal Callus Development in *Nautilus pompilius*

BY

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(1 Plate)

IN THE EARLY STAGES of his study of *Nautilus* in the Indo-Pacific, WILLEY (1896) reported several variations in conch morphology in *N. pompilius* for which he named several varieties. These varieties are based primarily on differences in the shape of the umbilical shoulder and umbilical callus – a calcium carbonate plug deposited within the umbilicus of the conch by the mantle. The taxonomic status of Willey's varieties is uncertain. He makes no mention of them as abnormal specimens, but terms them examples of "substantive variations" (WILLEY, 1896: 229).

In 1902, WILLEY (p. 811) viewed many variations in *Nautilus pompilius* as aberrations. However, he did not include any shell features in this category. It is therefore uncertain whether Willey intended his varieties to have subspecific or infrasubspecific rank in the modern sense.

With one exception, the specimens Willey reported as varieties had asymmetrical conchs; the exception being *Nautilus pompilius* variety *moretoni*, which was based on a single mature conch identical to *N. pompilius* in all respects other than its lack of umbilical calluses on both sides. MILLER (1947: 17) also reported asymmetrical callus development in *N. pompilius*, although it is unclear if this was a personal observation or a citation of Willey. Neither author attempted to explain the origin of the condition.

Recently, an unnumbered specimen similar to *Nautilus pompilius* var. *moretoni* was found in the collections of the Museum of Comparative Zoology at Harvard Uni-

versity. When this specimen is viewed from the right side, the shell appears to be that of a normal *N. pompilius* with a normal umbilical plug (Figure 1); when viewed from the left side, the conch appears to lack the callus (Figure 2) and looks like the specimen described by Willey as *N. pompilius* var. *moretoni* or the specimen referred to by SHIMANSKY & ZHURAVLEVA (1961) as *N. moretoni* Willey. Closer examination of this specimen indicates that there is an immature callus present deep within the left umbilicus. This suggests that mantle dysfunction at some time during growth was responsible for this abnormality. Our observations indicate that the callus usually begins to develop at the nepionic constriction (conch diameter = 22 to 27 mm) and the umbilical opening is completely closed by the time the animal makes a complete volution beyond the nepionic constriction (conch diameter = approximately 70 mm).

Thus, analysis of the Harvard specimen indicates that a callus had begun to form during the post-embryonic growth of the animal, and at least one complete volution before maturity, the portion of the mantle responsible for the formation of the umbilical callus was damaged. The reason for this mantle damage is not apparent. WILLEY (1902: 732, 739) reported predatory attacks on *Nautilus* by sharks and conger eels, and conjectured attacks by other *Nautilus* (p. 810). HAVEN (1972: 79) has reported intraspecific fighting in *Nautilus*. The possibility of parasitic damage of the mantle cannot be ruled out, although injury by this agency has not been reported as occurring

Explanation of Figures 1 to 3

Figure 1: Normal-appearing right side of conch of *Nautilus pompilius* (maximum diameter: 123 mm). approx. $\times 0.7$

Figure 2: Left side of the specimen in Figure 1. Note the apparent lack of an umbilical callus.

Figure 3: Close-up of the abnormal umbilicus of Figure 2. Note the white umbilical callus in the early, partly exposed juvenile stages. $\times 2$



Figure 1



Figure 2



Figure 3



in *Nautilus*. We feel that the lack of an umbilical callus is, in this instance, more likely explained as the result of non-regeneration of the mantle after injury.

Due to lack of population and geographic range data, the number of biologically meaningful species of *Nautilus* remains problematic. The presence or absence of an umbilical callus has been considered taxonomically significant by many workers. For example, STENZEL (1964: K88) divided the 5 generally recognized species of *Nautilus* into 2 groups on that basis.

Both Willey's specimen and that reported by Shimansky & Zhuravleva as *Nautilus moretoni* Willey are identical to *N. pompilius* except that they lack umbilical calluses. WILLEY (1897: 228) listed several characters as differentiating *N. moretoni* from *N. pompilius* (s. str.), but it is clear from both his description and figures that all could result simply from failure by an individual to develop umbilical calluses.

In order to clarify the position of *Nautilus moretoni*, it is necessary to examine the nomenclatural and taxonomic status of this "species." SHIMANSKY & ZHURAVLEVA (1961) appear to have elevated Willey's *Nautilus pompilius* variety *moretoni* to species status as *N. moretoni* Willey. Because their action was taken after some relevant sections of the International Code of Zoological Nomenclature took effect, it is only questionably valid. Under the present rules, varieties named after 1960 are, by definition, of infrasubspecific rank [article 45e(ii)] and hence cannot be elevated in rank according to the provisions of article 1 (STOLL *et al.*, 1963: 5, 47). A variety published prior to 1961 can be regarded as of subspecific rank if the original author "did not clearly state its rank" (article 45d(i): STOLL *et al.*, 1963: 45). This provision is probably applicable in this case, but its force is qualified by article 45e(i) (STOLL *et al.*, *op. cit.*): "Before 1961, the use of either the terms 'variety' or 'form' is not to be interpreted as an express statement of either subspecific or infraspecific rank."

According to MAYR (1969: 362) it is good taxonomic practice to "give the benefit of the doubt" to authors who introduced varieties prior to 1961. Possibly this is what SHIMANSKY & ZHURAVLEVA (1961) had in mind; but as no explanation was provided, this must remain conjectural. As we have stated above, from a morphologic standpoint, *Nautilus moretoni* is also suspect. *Nautilus pompilius* can lack one umbilical callus, and there is no

reason why both calluses could not also be missing. Thus, both Willey's specimen and that illustrated by Shimansky & Zhuravleva as *N. moretoni* Willey may be abnormal *N. pompilius* that failed to develop umbilical calluses, at least in later stages of growth. In our opinion, *N. moretoni* Willey is best regarded as being based on teratologic specimens and the name should be treated as a synonym of *N. pompilius* Linnaeus, 1758. As neither Willey's nor Shimansky & Zhuravleva's specimens were available to us for study, it remains to be investigated whether or not juvenile calluses are present on their specimens. Even if they are not present, recognition of a separate species solely on the basis of presence or absence of the umbilical calluses is probably not justified.

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Helpful editorial criticism and advice about *Nautilus* were provided by Brian F. Glenister. Gilbert Klapper contributed valuable suggestions concerning interpretations of the International Code of Zoological Nomenclature. Kathleen Lewis assisted in the translation of Shimansky & Zhuravleva's work. To all, our thanks.

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The Genus *Callistochiton* Dall, 1879

(Mollusca : Polyplacophora)

in the Eastern Pacific, with the Description of a New Species

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(3 Plates; 9 Text figures)

THE GENUS *Callistochiton* Dall, 1879, is particularly well represented in the eastern Pacific. Ten species are recognized here, 4 in the north temperate region (one new to science), 5 in the tropical region, and 1 in the south temperate region, distributed between 40°N and 20°S. The genus has representatives worldwide, mostly in the tropical belt, but nowhere with the abundance with which it is found on the west coast of the American continent.

The purpose of this paper is to review the taxonomic position of the eastern Pacific chiton species assigned to the genus *Callistochiton* and ascertain their currently known ranges of distribution. The work is based upon the chiton collections in the California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (LACM), Allan Hancock Foundation (AHF), National Museum of Natural History (USNM), Academy of Natural Sciences of Philadelphia (ANSP), University of California at Los Angeles (UCLA), San Diego Museum of Natural History (SDNH), American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), and the private collections of Glenn & Laura Burhardt, Salle Crittenden, George A. Hanselman, Allyn G. Smith (AGS), and Antonio J. Ferreira (AJF).

POLYPLACOPHORA de Blainville, 1816

Neoloricata Bergenhayn, 1955

ISCHNOCHITONINA Bergenhayn, 1930

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CALLISTOPLACIDAE Pilsbry, 1893

Callistochiton Dall, 1879

Tegmentum conspicuously sculptured; end valves and lateral areas of intermediate valves with strong radial ribs which, on closer examination, often appear as undulations rather than thickenings of the tegmentum; these "ribs" are often granose or tuberculated. Characteristically, the lateral areas are bicostate, and the end valves have no more than 10-12 ribs. The central areas of the intermediate valves are usually strongly sculptured, too, with longitudinal riblets, latticing, or a pitted appearance. The insertion plates tend to be relatively short; the insertion teeth are often thickened at the edges of the slits and festooned at the free edges. The slits tend to correspond in number and position to the ribs of the tegmentum. The intermediate valves are uni-slitted. The sutural laminae are relatively short, subquadrate to semi-oval; sinus relatively shallow. Girdle narrow, densely set with relatively small, imbricating scales. Gills as long as the foot.

Type species: *Callistochiton palmulatus* Dall, 1879, by M

Remarks: Many workers consider "Carpenter in Dall" as the proper authority for *Callistochiton*. Unquestionably, *Callistochiton* was Carpenter's manuscript name and arrangements as revealed not only by DALL (1879), TRYON (1883), and PILSBRY (1893), but through the examination of the relevant pages in Carpenter's unpublished manuscript in the repository of the National Museum of Natural History, Washington, D. C., made available to me through the kindness of Dr. Joseph Rosewater. But

since names proposed in unpublished manuscripts have no taxonomic standing, the fact remains that it was DALL (1879), who adopted and first published the name *Callistochiton*, defining the genus with the description and figure of the radula of *C. palmulatus*. Thus, there seems to be no justification for the dual authorship "Carpenter in Dall," often given to *Callistochiton*. It must be added that the case of *Callistochiton* differs from those where the second author gives the first author's description, or illustration, or both; for instance, in several species with the authorship "Carpenter in Pilsbry," such as *Lepidozona sinudentata*, the dual authorship is appropriate inasmuch as Pilsbry quotes directly from Carpenter's unpublished manuscript in a manner which makes it clear where Carpenter's contribution ends and Pilsbry's begins.

THIELE (1929: 18) placed *Callistochiton* as a subgenus in *Lorica* H. & A. Adams, 1852 (together with *Lorica* s. s. *Lepidozona* Pilsbry 1892, *Loricella* Pilsbry, 1892, and *Squamophora* Nierstraß, 1905), apparently on the basis of radular characteristics. This taxonomic arrangement has had no acceptance among chiton workers (FERREIRA, 1974).

Synonyms: *Lophochiton* Ashby, 1923 [not Berry, 1925], (Type: *Lophochiton johnstoni* Ashby, 1923, by OD); *Callistassecla* Iredale & Hull, 1925 (Type: *Callistochiton mawlei* Iredale & May, 1916, by OD); *Callistelasma* Iredale & Hull, 1925 (Type: *Chiton antiquus* Reeve, 1847, by OD).

Callistochiton palmulatus Dall, 1879

(Figure 1)

"*Callistochiton palmulatus* Cpr." DALL, 1879: 297; fig. 20 (radula)

Callistochiton palmulatus. HADDON, 1886: 20 - THIELE, 1893: 378; plt. 31, fig. 8 (radula) - PILSBRY, 1893, 14: 262 to 264; plt. 58, figs. 7-16 - BERRY, 1907: 52 - E. P. CHACE, 1917: 30 (Pleistocene) - DALL, 1921: 193 - JOHNSON & SNOOK, 1927: 564-565; fig. 663 - OLDROYD, 1927: 894 - T. A. BURCH, 1942: 7 - J. Q. BURCH & T. A. BURCH, 1943: 5, 7 - PALMER, 1945: 101 - A. G. SMITH, 1947: 18 - A. G. SMITH & GORDON, 1948: 208 - LELOUP, 1953: 17-18; fig. 11 (with syn. *Callistochiton palmulatus mirabilis* Pilsbry, 1893) - LIGHT'S Manual, 2nd ed., 1954: 217-218 - PALMER, 1958: 279; plt. 32, fig. 1 - G. & L. BURGHARDT, 1969: 12; plt. 1; figs. 7, 8 (with syn. *Callistochiton acinatus* Dall, 1919, and *C. celestus* Dall, 1919) - McLEAN, 1969: 63-64; fig. 35.4 - A. G. SMITH in Light's Manual, 3rd ed., 1974: 463, 464 - ABBOTT, 1974: 399 - A. G. SMITH, 1977: 217, 239-240

(with syn. *Callistochiton acinatus* Dall, 1919, *C. celestus* Dall, 1919, and *C. connellyi* Willett, 1937)

Callistochiton palmulatus mirabilis PILSBRY, 1893, 14: 263 to 264; plt. 58, figs. 7-11; 1898: 288 - BERRY, 1907: 52 - CHACE, 1917: 30 (Pleistocene) - DALL, 1921: 194 - BERRY, 1922: 409-412, 415, 489-492; tbl. 1; text fig. 11; plt. 14, figs. 9-16; plt. 15, figs. 1-14 (Pleistocene); 1926: 456 (Pleistocene) - OLDROYD, 1927: 894-895 - J. Q. & T. A. BURCH, 1943: 5 - A. G. SMITH, 1947: 18 - A. G. SMITH & GORDON, 1948: 208 - LELOUP, 1953: 17-18; fig. 11 (syn. of *C. palmulatus*) - LIGHT'S Manual, 2nd ed., 1954: 218 - A. G. SMITH, 1963: 148 - G. & L. BURGHARDT, 1969: 12 - A. G. SMITH in Light's Manual, 3rd ed., 1974: 464

Callistochiton acinatus DALL, 1919: 510; 1921: 194 - OLDROYD, 1927: 898 - A. G. SMITH, 1947: 18 - G. & L. BURGHARDT, 1969: 12 (syn. of *C. palmulatus*) - ABBOTT, 1974: 399 - A. G. SMITH, 1977: 217, 239 (syn. of *C. palmulatus*)

Callistochiton celestus DALL, 1919: 510-511; 1921: 194 - OLDROYD, 1927: 898 - A. G. SMITH, 1947: 18 - G. & L. BURGHARDT, 1969: 12 (syn. of *C. palmulatus*) - ABBOTT, 1974: 399 - A. G. SMITH, 1977: 217, 239 (syn. of *C. palmulatus*)

Callistochiton connellyi WILLETT, 1937: 25-26; plt. 2 fig. 13 - A. G. SMITH, 1947: 18 - A. G. SMITH & GORDON, 1948: 208 - G. & L. BURGHARDT, 1969: 11; plt. 1, fig. 4 - ABBOTT, 1974: 399 - A. G. SMITH, 1977: 217, 240 (syn. of *C. palmulatus*)

Description: Chitons with high-arched, rounded back. Length up to 1.5 cm. Color light creamy, often with greenish to gray specks. Anterior valve with 9-11 massive, somewhat pustulose, radial ribs. Posterior valve often raised and thickened by the presence of 4 to 6 unusually strong radial ribs; mucro anterior. Lateral areas of intermediate valves robustly bicostate. Central areas with some 15 longitudinal riblets per side, finely cross-ribbed. In the end valves, the sulci between the radial ribs are wide and coarsely pitted; similarly, pitted sulci separate the radial ribs in the lateral areas. Girdle often banded and covered with closely set, imbricating, oval scales about 150 μ m in length, with some 10-12 deep striations (Figure 1). Articulamentum white. Valves thick and massive. Sutural laminae semioval, sharp; sinus hardly formed, almost absent in the posterior valves. Insertion teeth short; in valve i there are 9-11 teeth, somewhat thickened at the edge of the slits, corresponding in position to the radial ribs of tegmentum; intermediate valves unisulcated; posterior valve conspicuously thick, with a close series of small, irregularly shaped teeth, about 20 in number.

The radula is figured in DALL (1879: fig. 20), and THIELE (1893: plt. 31, fig. 8). Dall's description of the

major lateral as having "a simple cusp" (DALL, *op. cit.*: 297) is not correct; as Thiele's illustration shows, there are 2 cusps, a large inner cusp, and a small outer one. The examination of the radulae of 6 specimens of *Callistochiton palmulatus* from several localities corroborated the anatomical details shown in Thiele's figure; Dall's figure is compatible with Thiele's and my own observations except for the description of the cusp of the major lateral. However, the difficulties of correctly observing the radula, particularly if the specimen happens to be small, may easily explain the discrepancy; in addition, if viewed from the side the cusp may look single and simple, as Dall illustrated and described. A specimen of *C. palmulatus* (Monterey Bay, California, leg. A. J. Ferreira, at 20 m, June 30, 1977, AJF 342), measuring 16.2 mm in length, has a radula 6.3 mm long, *i. e.*, 39% of the specimen's length with 40 rows of mature teeth. The median tooth is 135 μ m long, enlarged anteriorly where it bears a thin blade about 95 μ m wide. First lateral has the characteristic knob in the outer-anterior corner. The major lateral is bicuspid, the larger inner cusp measuring 125 μ m in length. Outer marginal teeth are elongated, measure 115 μ m in length, 75 μ m in width.

Type Material: Dall limited himself to a description of the radula; his material could not be located either at the National Museum of Natural History, or at the Academy of Natural Sciences of Philadelphia, and is presumed lost. The first complete description of the species comes from PILSBRY (1893: 14: 262-263) based on Carpenter's manuscript description, drawings and specimens. The description corresponds to a specimen in the Carpenter Collection in the Redpath Museum, Canada, bearing the label "type, Sta. Barbara, Cooper no. 1077" (*vide* PALMER, 1958: 279). The specimen is regarded as a holotype by PALMER (*loc. cit.*). Since the author of *Callistochiton palmulatus* is Dall, not Carpenter, Palmer's designation under the present rules of the ICZN is incorrect; the radula, or, rather the specimen from which the radula was obtained, that served Dall as the basis for his "description," would be the holotype. In the interest of the stability of nomenclature and fixation of the concept of the species *C. palmulatus*, the specimen illustrated by PALMER (*op. cit.*: pl. 32, fig. 1), and described in PILSBRY (*op. cit.*: 262-263) is herein designated as a neotype. The specimen, as stated by PALMER (*op. cit.*: 279) measures 8 mm in length and 7 mm in width; it is preserved dry, with valves i, vii, and vii separated, as Redpath Museum no. 48.

Callistochiton palmulatus mirabilis Pilsbry, 1893: syn-types (ANSP 118682): type locality, San Diego, California.

Callistochiton acinatus Dall, 1919: holotype (USNM 218733); type locality, San Pedro, California.

Callistochiton celetus Dall, 1919: lectotype and paralectotype (USNM 218770); type locality, San Pedro, California.

Callistochiton connellyi Willett, 1937: holotype (LACM 1048), and several paratypes; type locality, "Arbolitos Point, near Ensenada, Lower California, Mexico."

Type Locality: The locality of Dall's original specimen is unknown. The locality of the neotype specimen, as given by PILSBRY (1893) and PALMER (1958) is Santa Barbara [34°25'N, 119°42'W], Santa Barbara County, California.

Distribution: Seemingly continuous between parallels 39° N and 27° N. The northernmost record is Buckhorn Creek [39°17'N, 123°48'W], Mendocino County, California (CASG 32233). The southernmost record is San Pablo Point [27°12'N, 114°29'W], Baja California, Mexico (LACM 71-178). The species has been collected at most offshore islands, namely Santa Rosa (LACM-AHF 1282-41), Santa Cruz (LACM 96-32), Anacapa (LACM AHF 1421-41), Catalina (LACM 64-26), San Nicolas (LACM-AHF 1694-49), San Clemente (LACM-AHF 66-51), Coronados (LACM 63-41), Natividad (LACM 72-116), San Gerónimo (LACM 71-91), San Martin (LACM-AHF 1694-49), Guadalupe (CASG 32746), and Cedros (LACM 72-115). Known bathymetric range extends from the intertidal zone to 40-50 fathoms [73-82 m] (LACM-AHF 1297-41).

Fossil Record: Pleistocene deposits in southern California (CHACE, 1917; BERRY, 1922), in San Quintín, Lower California, Mexico (BERRY, 1926) and in Guadalupe Island (FERREIRA, 1978a).

Remarks: The subspecies *Callistochiton palmulatus mirabilis* Pilsbry, 1893, is suppressed here as a synonym, as already suggested by LELOUP (1953: 17-18). The observation of many intergradations between the 2 morphs "*palmulatus*" *s. s.* and "*mirabilis*," and their total lack of correlation to locality or depth demonstrate that the forms of tail valve and mucro represent intraspecific variation with no taxonomic significance. *Callistochiton acinatus* Dall, 1919 and *C. celetus* Dall, 1919 were found to be synonyms of *C. palmulatus* upon examination of the respective type material (A. G. SMITH, 1977: 239). The synonymy of *C. connellyi* Willett, 1937, already indicated by A. G. SMITH (*op. cit.*: 240), was reaffirmed upon examination of the holotype through the courtesy of Dr. James H. McLean.

Callistochiton crassicostatus Pilsbry, 1893

(Figures 2, 3)

Callistochiton crassicostatus PILSBRY, 1893, 14: 264-265; plt. 58, figs. 1-6; 1898: 288 - BERRY, 1907: 52 - E. P. CHACE, 1917: 30 (Pleistocene) - E. P. & E. M. CHACE, 1919: 2 (Pleistocene) - DALL, 1921: 194 - BERRY, 1922: 409-410, 412, 414, 484-488; tbl. 1; text fig. 10; plt. 13, figs. 1-16 (Pleistocene) - OLDROYD, 1924: 194 - BERRY, 1926: 456 (Pleistocene) - JOHNSON & SNOOK, 1927: 565; fig. 665 - OLDROYD, 1927: 895 - STRONG, 1937: 194 - T. A. BURCH, 1942: 7 - A. G. SMITH, 1947: 18 - A. G. SMITH & GORDON, 1948: 208 - LA ROCQUE, 1953: 12 - LELOUP, 1953: 5-6; fig. 8 - LIGHT'S Manual, 2nd ed., 1954: 217-218 - G. & L. BURGHARDT, 1969: 11-12; plt. 1, fig. 5 - McLEAN, 1969: 63; fig. 35.2 - ABBOTT, 1974: 399 - A. G. SMITH in Light's Manual, 3rd ed., 1974: 463-464

"*Callochiton fimbriatus* Cpr." COOPER, 1867: 23 [*nomen nudum*] [not *Chiton fimbriatus* Sowerby, 1840]

"*Chiton (Callochiton) fimbriatus* Cpr." ORCUTT, 1885: 544 [*nomen nudum*]; 1915: 23 [*nomen nudum*]

"*Callistochiton fimbriatus*' Carpenter, MS, *nomen nudum*" PALMER, 1958: 278

Description: Chiton with high arched, round back. Length up to 3 cm. Color creamy tan to gray or light green. Anterior valve with 7 strong, somewhat granose radial ribs, each often divided by 1-4 sulci which become more apparent towards the periphery. Posterior valve with 5 equally strong radial ribs, again often subdividing at the periphery; mucro well defined at the posterior edge of the valve with markedly sloped, almost vertical, and convex postmucro. Lateral areas of intermediate valves with a single, very strong radial rib, usually subdivided by 4-6 sulci; the radial ribs often show concentric annulations, about 12 per rib, which together with the radial sulci tend to divide the single rib into coarse granules. Central areas have longitudinal riblets, about 12 per side, which remain parallel to the jugum or may converge slightly anteriorly; the riblets are finely cross-ribbed. Girdle narrow, often banded and covered with close set, imbricating oval scales, about 100-120 μ m in length, with some 6-8 deep striations (Figure 2). Articulamentum is white or bluish-white. Sutural laminae thin, semioval, separated by a relatively small, rounded sinus. Anterior valve with 8-9 very short teeth, thickened at the edges, festooned at the free edge; intermediate valves uni-slitted; posterior valve very thick and massive, with a series of 12-20 very short teeth, usually blunt and irregular in shape and size.

The radula of a specimen of *Callistochiton crassicostatus* 23.0 mm long (Monterey Bay, California, leg. A. J. Ferreira, September 1973, at 13 m, AJF 89) measures 8.0 mm in length, i. e., 35% of the specimen's length. It

has 48 rows of mature teeth, morphologically very similar to those of *Callistochiton palmulatus*. The median tooth is enlarged in front (where it bears a blade, 125 μ m in width) and narrows posteriorly to about 50 μ m; in length it measures about 200 μ m. The first laterals are subquadrate, with a knobby protuberance in the outer-anterior corner. The major (2nd) lateral has a bicuspid head, the inner cusp somewhat larger than the outer cusp (Figure 3); the head measures about 100 μ m in width, and 100 μ m in the length of the longest (inner) cusp. Outer marginal teeth are elongated, 140 μ m long and 100 μ m wide.

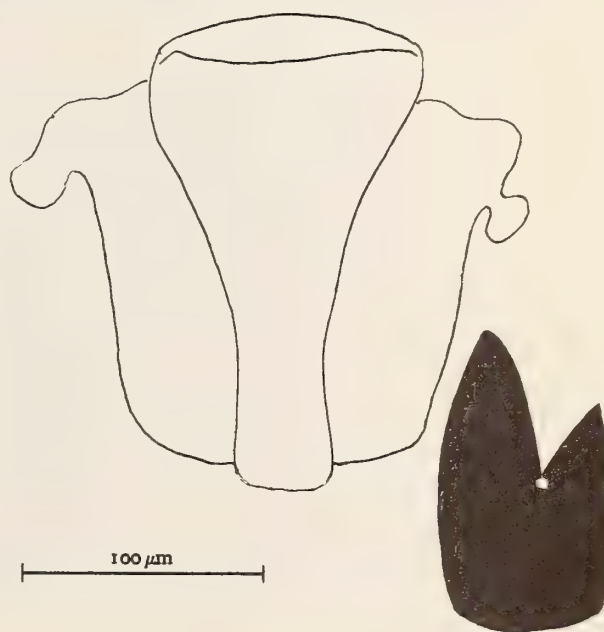


Figure 3

Callistochiton crassicostatus Pilsbry, 1893

Radula: Median tooth, first lateral teeth, and head of second lateral tooth. Specimen collected at Monterey Bay, California (AJF 89), original length 23.0 mm

Type Material: Syntype series (ANSP 118683), composed of 3 specimens, 1 wholly disarticulated but with girdle (Dr. Robert Robertson, *in litt.*, 24 August 1976). The disarticulated specimen, very likely the one illustrated by PILSBRY (1893, 14: plt. 58, figs. 4-6), is here designated as lectotype.

Type Locality: "Monterey [36°37'N, 121°55'W], California" as stated by PILSBRY (1893, 14: 265).

Distribution: Apparently continuous between parallels 36°N and 31°N. The northernmost record from the available collections is Trinidad [41°04'N, 124°10'W], Humboldt County, California (Glenn & Laura Burghardt Collection, *in litt.*, 9 August 1975); reported records from farther north, such as Puget Sound, Washington (OLDROYD, 1924: 194), and Forrester Island, Alaska (DALL, 1921: 194) have not been confirmed. *Callistochiton crassicosatus* is particularly abundant from Monterey Bay to San Diego, California. The verified southernmost record is Cedros Island [28°10'N, 115°15'W], Baja California, Mexico (SDNH 23474, *leg.* H. N. Lowe). On the offshore islands it has been collected at Santa Cruz (LACM-AHF 1660-48), San Miguel (CASG 13778), Catalina (LACM-AHF 1903-49), and Coronados (LA CM 63-41). Bathymetrically, it has been recorded from the intertidal zone to 27 - 31 m (LACM-AHF 1903-49). An unusual finding was the collection of a single specimen, estimated length 2.5 cm, at "400-350 fathoms [732 to 640 m] on mud, 11 miles [17.6 km] northeast of Avalon, Santa Catalina Island, Los Angeles County, California (33°27'24"N, 118°10'53"W), August 11, 1951," (LA CM-AHF 2049-51). It is also of interest to note that in the available collections I found no instance of the species having been collected between Punta Banda (31°43'N, 116°43'W), Baja California, Mexico (LACM 63-42), and the Cedros Island site, some 3° south, mentioned above.

Fossil Record: Pleistocene deposits in San Quintín, Lower California, Mexico (BERRY, 1926); Santa Monica Hills (CHACE, 1917), and San Pedro (CHACE & CHACE, 1919; BERRY, 1922) in southern California.

Remarks: The taxonomic position of "*Callistochiton fimbriatus*," a Carpenter manuscript name, has been sufficiently clarified in PILSBRY (1893, 14: 265 - 266) and PALMER (1958: 278 - 279) so as to require no further comment.

Callistochiton decoratus Pilsbry, 1893

"*Chiton (Callistochiton) decoratus* Cpr." ORCUTT, 1885: 544
[*nomen nudum*]

"*Callistochiton decoratus* Carpenter, n. sp." PILSBRY, 1893, 14: 269 - 270; pl. 58, figs. 17 - 20

Callistochiton decoratus. E. P. CHACE, 1917: 44 - E. P. & E. M. CHACE, 1919: 2 (Pleistocene) - DALL, 1921: 194 - OLDROYD, 1927: 896 - T. A. BURCH, 1942: 7 - PALMER, 1945: 101 - A. G. SMITH, 1947: 18 - LELOUP, 1953: 6 - 7; fig. 4 - PALMER, 1958: 278; pl. 33, figs. 15 - 21 - G. & L. BURGHARDT, 1969: 12; pl. 1, fig. 6 (with syn.: *C. chthonius* and *C. cyanosus*) - McLEAN, 1969: 63; fig. 35-3 - ABBOTT, 1974: 39 (with syn. *C. punctocostatus*, *C. ferminicus*, *C. chthonius*, and *C. cyanosus*) - A. G. SMITH, 1977: 217, 240 (with syn. *C. cyanosus*, *C. decoratus punctocostatus*, and *C. chthonius*)

Callistochiton decoratus punctocostatus PILSBRY, 1896: 50 - DALL, 1921: 194 - BERRY, 1922: 409, 418, 481-483; tbl. 1; pl. 14, figs. 1 - 6 (Pleistocene) - OLDROYD, 1927: 897 - A. G. SMITH, 1947: 18 - A. G. SMITH & GORDON, 1948: 208 - G. & L. BURGHARDT, 1969: 12 - ABBOTT, 1974: 399 (syn. of *C. decoratus*) - A. G. SMITH, 1977: 217, 240 (syn. of *C. decoratus*)

Callistochiton decoratus ferminicus BERRY, 1922: 483; pl. 14, figs. 7 - 8 (Pleistocene) - ABBOTT, 1974: 399 (syn. of *C. decoratus*)

Callistochiton diegoensis THIELE, 1910: 86 - 87; pl. 9, figs. 4 - 10 - DALL, 1921: 194 - OLDROYD, 1927: 897 - A. G. SMITH, 1947: 18 - ABBOTT, 1974: 399

Callistochiton cyanosus DALL, 1919: 511; 1921: 194 - OLDROYD, 1927: 900 - A. G. SMITH, 1947: 18 - G. & L. BURGHARDT, 1969: 12 (syn. of *C. decoratus*) - ABBOTT, 1974: 399 (syn. of *C. decoratus*) - A. G. SMITH, 1977: 217, 240 (syn. of *C. decoratus*)

Callistochiton chthonius DALL, 1919: 511 - 512; 1921: 194 - OLDROYD, 1927: 900 - A. G. SMITH, 1947: 18 - G. & L. BURGHARDT, 1969: 12 (syn. of *C. decoratus*) - ABBOTT, 1974: 399 (syn. of *C. decoratus*) - A. G. SMITH, 1977: 217, 240 (syn. of *C. decoratus*)

Description: Chitons with relatively low-arched, round backs. Length up to 3 cm. Color usually uniform olive-green to tan, often with darker flecks. Anterior valve with 10 - 12 rounded radial ribs, of a relatively smooth surface except for some occasional growth rings; radial ribs separated by very well defined and pitted sulci. Posterior valve with 8 - 10 similar radial ribs; mucro well defined, slightly posterior. Lateral areas of intermediate valves bicostate, again with the 2 rounded ribs separated by a pitted sulcus. Central areas with 8 - 12 longitudinal rib-

Explanation of Figures 1, 2, 4, 5, 16, 17

Figure 1: *Callistochiton palmulatus* Dall, 1879. Girdle scales. SEM micrograph by Dennis Nichols and Myrl Stone × 700

Figure 2: *Callistochiton crassicosatus* Pilsbry, 1893. Girdle scales. SEM micrograph by Dennis Nichols and Myrl Stone × 300

Figure 4: *Callistochiton asthenes* (Berry, 1919). Girdle scales. SEM micrograph by Hans Bertsch × 300

Figure 5: *Callistochiton asthenes*. Girdle scales. SEM micrograph by Hans Bertsch × 1000

Figure 16: *Callistochiton colimensis* (A. G. Smith, 1961). Cuastocoma, Jalisco, Mexico (LACM 68-41). Length 17 mm

Figure 17: *Callistochiton colimensis*. Girdle scales. SEM micrograph by Hans Bertsch × 620



Figure 1



Figure 2



Figure 4

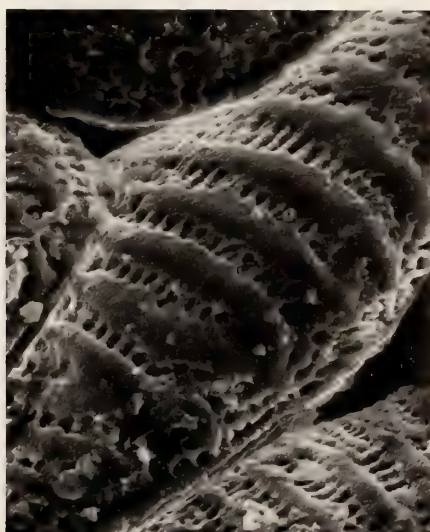


Figure 5

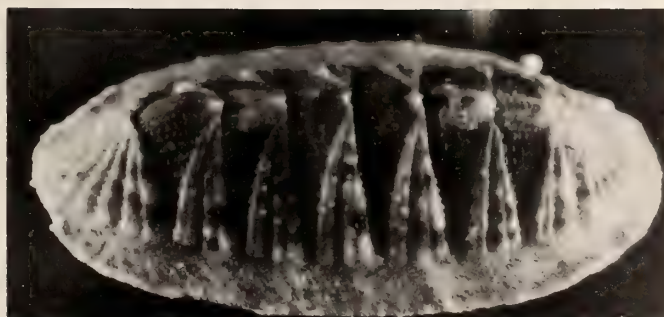


Figure 16



Figure 17



lets per side, parallel (or slightly divergent anteriorly), neatly cross-ribbed for a latticed effect. Jugum usually smooth (*i. e.*, not ribbed, the ribs having become obsolete), often lustrous and shiny, as if polished, a tegmental characteristic sometimes also noticed on the surface of the radial ribs of the end valves and lateral areas. Girdle, often banded, tan or dark green. Girdle scales strongly imbricated, oval, measuring about 160 - 200 μm in length, and showing 8 - 10 deep striations. Articulamentum white to bluish, often with a dark brown discoloration at the apex of the valve, particularly on valve viii. Sutural laminae relatively wide and semioval; sinus well defined, the sinusal lamina with a few irregular pectinations, usually separated by a small notch from the adjacent sutural laminae. Anterior valve with 9 - 11 teeth, thickened at the edges, festooned at the free edges; intermediate valves uni-slitted; posterior valve with 9 - 11 similar teeth. In some specimens the insertion plate of the posterior valve may be divided into very small teeth (over 25 in one small specimen examined), often short, irregular in shape and size, and not continued by a slit ray.

The radula is very similar to those of *Callistochiton pal-mulatus* and *C. crassicosatus*. A specimen 21 mm in length (San Clemente Island, California, *leg.* A. J. Ferreira, 26 October 1975, at 10 m, AJF 252) has a radula measuring 6.7 mm in length, *i. e.*, 32% relative size, with 70 rows of mature teeth. Median tooth large in front (100 μm) where it has a small blade, tapers posteriorly; length of the tooth about 125 μm . First lateral teeth have a knobby protuberance in the outer-anterior corner. Second lateral has a bicuspid head about 50 μm in width; the inner cusp, the longest of the 2, is about 100 μm in length. The outer marginal teeth are elongated, measuring 100 μm in length, 80 μm in width.

Type Material: Holotype (ANSP 118687). "Although Pilsbry utilized Carpenter's manuscript name for this species, he did not use Carpenter's description or his type. Pilsbry's type was a specimen in the Academy of Natural History, Philadelphia." (PALMER, 1958: 278).

Callistochiton diegoensis Thiele, 1910: Holotype (Zoologisches Museum, Berlin). Color slides at CASIZ nos. 3339-3340

Callistochiton decoratus punctocostatus Pilsbry, 1896: Syntypes (ANSP 118689)

Callistochiton chthonius Dall, 1919: Holotype (USNM 109488)

Callistochiton cyanosus Dall, 1919: Holotype (USNM 109317)

Type Locality: "Todos Santos Bay and near San Tomas River [31°48'N, 116°42'W], Lower California" (PILSBRY, 1893, 14: 269).

Distribution: Continuous between parallels 34° N and 31° N. Northernmost record, Point Arguello [34°25'N, 120°39'W], Santa Barbara County, California (CASIZ 006298); southernmost record, Isla Cedros [28°10'N, 115°15'W], Baja California, Mexico (SDNH 23226). *Callistochiton decoratus* has also been collected at the offshore islands of Santa Cruz (AJF, December 1970), Santa Rosa (LACM 73-9), Anacapa (LACM M-41), Santa Barbara (LACM 72-97), Catalina (LACM-AHF 1652-48), San Clemente (LACM-AHF 1021-39), and Coronados (LACM A-5757). It is interesting to note that, just as with *C. crassicosatus*, there has been no recorded collection of *C. decoratus* between Punta China (31°33'N, 116°40'W), Baja California, Mexico (LACM-AHF 1596-47), and Cedros Island, some 3° south. The presence of *C. decoratus* in the Gulf of California, "... reported ... from La Paz by Carpenter (Pease coll.)" (PILSBRY, 1893, 14: 270), has never been confirmed. The known bathymetrical range of *C. decoratus* extends from the low intertidal zone to about 72 m (LACM-AHF 1191-40-D1, Santa Cruz Island).

Fossil Record: Pleistocene deposits in San Pedro, southern California (CHACE & CHACE, 1919; BERRY, 1922).

Remarks: The subspecies *Callistochiton decoratus punctocostatus* Pilsbry, 1896, is here placed in synonymy inasmuch as the alleged sculptural differences fall well within the range of intraspecific variation accorded to *C. decoratus*, as already noted by LELOUP (1953: 6-7), and A. G. SMITH (1977: 240). The synonymization of *C. cyanosus* Dall, 1919 and *C. chthonius* Dall, 1919, follows from Dall's original description, and the study of the holotypes, as reported by A. G. SMITH (*op. cit.*: 239-240).

The type material of *Callistochiton diegoensis* Thiele, 1910, consists of a single specimen preserved in alcohol in the repository of the Zoologisches Museum, Berlin, Deutsche Demokratische Republik. The specimen was made available for study through the generosity of Dr. R. Kilias; it measures 17.0 mm in length and corresponds in every detail to the description and illustration provided by THIELE (1910); valves i, v, and viii, disarticulated and segregated in a vial, are those figured by THIELE (*op. cit.*, plt. 9, figs. 4-10). The specimen is unquestionably conspecific with *C. decoratus*; although the tegmental features are a bit sharper than usual, the deviation is well within the known intraspecific variation of the species.

Callistochiton decoratus ferminicus Berry, 1922, was placed in the synonymy of *C. decoratus* by LELOUP (1953); indeed, the stated distinctions would hardly justify a new name, particularly in view of the fact that, as Berry himself acknowledged, *C. decoratus* "is so extraordinarily variable a chiton" (BERRY, 1922: 483).

Callistochiton asthenes (Berry, 1919)

(Figures 4, 5, 6)

Ischnochiton (*Lepidozona*) *asthenes* BERRY, 1919a: 7; 1919b: 18-21; pl. 8, figs. 1-2*Ischnochiton asthenes*. DALL, 1921: 192 (in section *Lepidozona*)*Lepidozona asthenes*. A. G. SMITH, 1963: 148-149; 1966: 438-442 - G. & L. BURGHARDT, 1969: 20 - ABBOTT, 1974: 395*Callistochiton asthenes*. FERREIRA, 1978b: 39

Description: Chitons moderately elevated and slightly carinated. Length up to 1 cm. Tegmental surface microgranulose. Color cream to light brown. Anterior valve with 11-12 very low, broad, radial ribs, often very indistinct except at the periphery of the valve; in some specimens a radial series of 2-4 minute pustules (apparently easily abraded) may be observed cresting the radial ribs. Posterior valve with mucro anterior; post-mucro area with radial ribs similar to those in anterior valve, only usually much weaker and less distinct, obsolete in some specimens. Intermediate valves with lateral areas clearly raised in most specimens, bicostate, the ribs broad and flattened, bearing a series of 2-4 minute pustules. These pustules (or tubercles) are absent in most specimens examined, either because they are easily abraded (as BERRY, 1919, suggested), or perhaps because they had not (yet?) developed. Central areas with some 15 finely sculptured longitudinal riblets, subtly interlaticed; these riblets are not present in young specimens, and in older (larger) ones become obsolete towards the jugum which appears devoid of sculpturing except for the rather "scaly" microgranulose appearance of the tegmental surface. Articulation white. Sutural laminae thin and broadly arcuate; sinus small. Insertion teeth sharp, very slightly festooned and somewhat thicker at the edges. Slit formula of a specimen from the type locality: 9-1-9. Girdle covered with imbricated, oval, rather small scales (about 150 μ m in length), with about 10 ribs separated by neatly pitted striations (Figures 4, 5).

The radula is figured here for the first time (Figure 6). In a specimen 7.6 mm long (CASG 38607, White's Point, Los Angeles County, California, *leg.* W. J. Raymond, 1901), the radula measures 2.8 mm long (36%) and is composed of 36 rows of mature teeth. The median tooth is large in front (58 μ m in width) where it bears a thin blade, and tapers posteriorly; its length is about 70 μ m. First lateral teeth are rectangular with a knobby protuberance in the outer-anterior corner. Second (major) lateral has a bicuspid head which is about 45 μ m in width

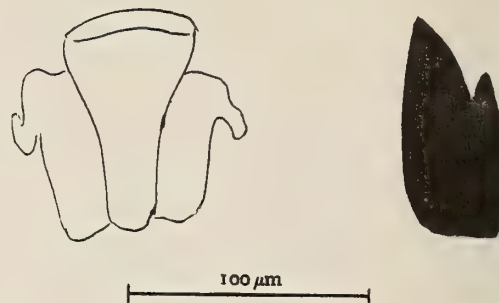


Figure 6

Callistochiton asthenes (Berry, 1919)

Radula: Median tooth, first lateral teeth, and head of second lateral tooth. Specimen collected at White's Point, California (CASG 38607), original length 7.6 mm

and 70 μ m in the length of the largest (inner) cusp. Outer marginal teeth are elongated, 75 μ m long, 45 μ m wide.

Type Material: Holotype, "preserved dry (S. S. B. 466), entered as Cat. No. 3913 in the author's [S. S. Berry] collection" (BERRY, 1919b: 20). Paratypes at USNM (332789), ANSP, CAS, and in A. G. Smith's private collection [now at CAS].

Type Locality: "Under stones at low tide, White's Point [33°42'N, 118°19'W], Los Angeles County, California" (BERRY, 1919b: 20).

Distribution: *Callistochiton asthenes* has been collected only in the general area of the type locality, Palos Verdes Peninsula, California, San Diego, California (SDNH 11637), and in the Coronados Islands, Guadalupe Island and Cedros Island, off the outer coast of Baja California, Mexico. From the type locality, the following lots were studied: 14 specimens, *leg.* W. J. Raymond 1901 (CASG 38607); "part of the type lot," *leg.* A. G. Smith 14-18 August 1916, 3 specimens (CASG 37998), and 11 specimens (CASG 43918); 10 specimens, July 1917 (SDNH 53830); 3 specimens, *leg.* E. P. Chace, 7 May 1950 (G. A. Hanselman Collection); 7 specimens *ex* George Willett Collection (UCLA 22402); 2 specimens, *leg.* S. Thorpe, July 1957 (LACM M-96). Recent attempts to collect the species at the type locality by myself (April 1974) and others (G. A. Hanselman, *in litt.*, 17 August 1974) have failed.

At Guadalupe Island (29°00'N, 118°16'W) *Callistochiton asthenes* was first collected by M. Woodbridge Williams, 7 December 1946, as a lot of 80+ specimens from a "tide pool at the south end" of the island (CASG 32746). On a recent expedition to Guadalupe Island, Dr. Welton L. Lee and I collected *C. asthenes* at 2 stations: 13 specimens at Northeastern Anchorage, 30 December 1974 (AJF 210), and 60 specimens at Sealers' Camp on the east side of the Island, 1-2 January 1975 (AJF 211).

From Coronado del Sur, Islas Los Coronados [32°25'N, 117°15'W] only one lot was found, composed of 2 specimens, 5 and 6 mm long, "ex Stephens Colln." (SDNH 53867).

From Cedros Island, Baja California, Mexico (28°10'N, 115°15'W), only 1 specimen was examined (SDNH 23625).

Callistochiton asthenes has only been collected in the intertidal zone, on the underside of rocks.

Remarks: *Callistochiton asthenes* joins the list of chitons that brood the young in the branchial groove (HYMAN, 1967: 114). Several of the specimens in the type lot (CASG 43918), and in the first lot collected at Guadalupe Island (CASG 32746) were observed to have several young specimens in the branchial groove.

One young in the branchial groove of *Callistochiton asthenes* 6.2 mm long was measured as 0.30 × 0.22 mm in size; it did not seem to have a (visible) girdle. Another of these young specimens had only 7 distinct valves. The significance of the brooding habit as exhibited by *C. asthenes* and many other species of chitons is not immediately apparent, although it has been regarded as "some stage in the development of viviparity" (DELL, 1965: 513) in chitons. It is a curious fact that none of the 73 specimens of *C. asthenes* collected at Guadalupe Island on 30 December 1974 to January 1975, at 2 different stations (AJF 210, 211) had young in the branchial grooves.

In length, *Callistochiton asthenes* does not usually attain 9 mm; the largest specimen examined measures 10.0 mm long (SDNH 23625).

Callistochiton leei Ferreira, spec. nov.

(Figures 7, 8, 9, 10, 11, 12)

Diagnosis: Very small (up to 8.5 mm long) chitons, mostly dark red maroon in color (Figure 7). End valves with about 12, lateral areas with 2-3 radial ribs which are well defined and granose. Central areas with 6-9 longitudinal riblets per side, with no latticing. Mucro anterior. Girdle often banded maroon and white. Girdle scales oval, smooth surfaced with no striations. Sutural

laminae sharp subquadrate. Slits corresponding to ribs; slit formula (holotype): 10-1-10.

Description: Holotype—When dried and fully extended, it measures, including girdle, 8.1 mm in length and 4.3 mm in width. Tegmentum uniformly dark "red wine" maroon. Anterior valve has 11 well defined radial ribs, strongly granose to the point of appearing tuberculated. These radial ribs are more like undulations of the tegmentum than "added on" ribs; they are seen to undulate the anterior margin of the valve. In the intermediate valves, the lateral areas show 2 similar radial ribs, well separated at the periphery. The central areas have some 8 well defined, slightly granose longitudinal riblets per side; there is no latticing, the space between the longitudinal riblets is wide, but featureless except for the microgranular surface that characterizes the whole tegmentum. The jugum is relatively smooth, *i. e.*, not ribbed. The posterior valve has an anterior mucro which, although well defined, is not too salient. The post-mucro area shows some 11 poorly marked, almost obsolete radial ribs. The articulamentum is white, somewhat translucent, the dark color of the tegmentum to shine through. The sutural laminae are moderately developed, sharp, thin, subquadrate. The sinus is relatively wide, and shows a minute sinusal lamina which, in some of the valves, displays a few discrete pectinations. The eaves are short and solid. The insertion plates are cut into teeth, with a slit formula 10-1-10. The teeth are slightly thickened at the edges, and very slightly festooned. The slits correspond in position to the radial ribs (undulations) of the tegmentum.

The girdle is faintly banded maroon and white. The girdle scales are oval, closely imbricated, about 150 μm in length; their outer surface is micropunctate with a sieve-like appearance, and no striations or other ornamentations (Figures 8, 9, 10). There is a marginal fringe of spicules about 50-60 μm long.

The gills extend the whole length of the foot.

The radula (Figure 11) measures 2.7 mm in length, *i. e.*, 34% of the specimen's length, and has 80 rows of mature teeth. The median tooth is quadrangular, measuring 37 μm in width by about 55 μm in length; it bears a relatively large blade on its anterior edge. The first lateral has a pointed prolongation on its outer-anterior corner; but its overall configuration is very difficult to determine with certainty in the preparation at hand. The second (major) lateral is tricuspid. The head is about 25 μm in width and 35 μm in the length of its middle (longest) cusp. The outer-marginal teeth are somewhat rounded, measuring 35 μm in length by 25 μm in width.

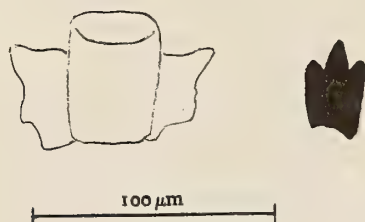


Figure 11

Callistochiton leei Ferreira, spec. nov.

Radula: Median tooth, first lateral teeth, and head of second lateral tooth. Holotype, Guadalupe Island, Baja California, Mexico (AJF 211), original length 8.1 mm

Type Material: Holotype (disarticulated valves, fragment of girdle, and mounted radula), is deposited at the California Academy of Sciences (CASIZ Type Series No. 705). Paratypes are deposited with the California Academy of Sciences (CASIZ Type Series No. 706); Natural History Museum of Los Angeles County (LACM 1905); National Museum of Natural History (USNM 749083); Academy of Natural Sciences of Philadelphia (ANSP 346418); American Museum of Natural History (AMNH 183817).

Color slides of paratypes are deposited at CASIZ, Color Slide Series.

Type Locality: Guadalupe Island, on the outer coast of Baja California, Mexico, at "Sealers' Camp," about the midpoint on the east side of the island (29°01'N, 118°13'W), where the holotype and 6 paratypes were collected at low tide in less than 1 m of water, by Welton L. Lee and Antonio J. Ferreira, 2 January 1975 (AJF 211).

Remarks: *Callistochiton leei* is known only from the type locality. The specimens collected were all about the same color, a dark maroon, with white along the jugum and central areas in some specimens; in size they varied between 8.5 and 4.8 mm in length, including girdle. With

C. asthenes, *C. leei* shares the habit of brooding the young. Four of the 7 specimens collected had minute juvenile chitons in the branchial grooves: one specimen had 2, one 3, one 8, and another 12 young. It is likely that there may have been more young chitons in the specimens collected, which may have fallen off during the collecting and preserving process that preceded examination. The young chitons measure about 500 μm in length; all are white. They show all 8 valves distinctly, but seem to have no visible girdle (Figure 12). The finding that *C. leei* broods the young seems all the more remarkable when it is considered that these specimens share the habitat with *C. asthenes*, a species also known for brooding its young; yet, among the 60 specimens of *C. asthenes* collected at the same station (AJF 211), and 13 more collected at a nearby station (AJF 210), none was found to carry young in the branchial groove. This observation suggests that *C. leei* and *C. asthenes* have different breeding seasons.

Although *Callistochiton leei* seems to be closely related to *C. asthenes*, they are absolutely distinct in color, sculpture of tegmentum, and girdle scales.

Callistochiton leei is endemic to Guadalupe Island, as is *Lepidozona guadalupensis* Ferreira, 1978. Based on a list of the chiton species previously known on the island (A. G. SMITH, 1963), the finding of *C. leei* raises the percentage of chiton endemism at Guadalupe Island to 20%.

The species is called *leei* after Dr. Welton L. Lee, Chairman, Department of Invertebrate Zoology, California Academy of Sciences, who shared in the collecting of the species at Guadalupe, and who has helped me generously and enthusiastically in every phase of this and other works.

Callistochiton gabbi Pilsbry, 1893

(Figures 13, 14, 15)

Callistochiton gabbi PILSBRY, 1893, 14: 270-271; pl. 60, figs. 7-10 - PILSBRY & LOWE, 1932: 129 - [?] BERGENHAYN, 1936: 282-284; text figs. 3a-3e [misidentified] - KEEN,

Explanation of Figures 7 to 10 and 12

Figure 7: *Callistochiton leei* Ferreira, spec. nov. Paratype. 8.5 mm long

Figures 8, 9, and 10: *Callistochiton leei* Ferreira, spec. nov. Holotype. Girdle scales. SEM micrographs by Hans Bertsch, × 100, × 300 and × 600, respectively

Figure 12: *Callistochiton leei* Ferreira spec. nov. Young specimen, about 500 μm in length. SEM micrograph by Hans Bertsch × 160



Figure 7

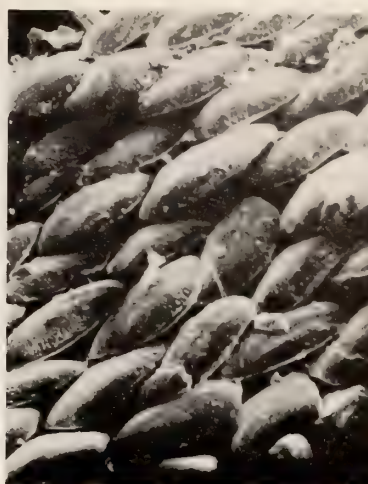


Figure 8



Figure 9

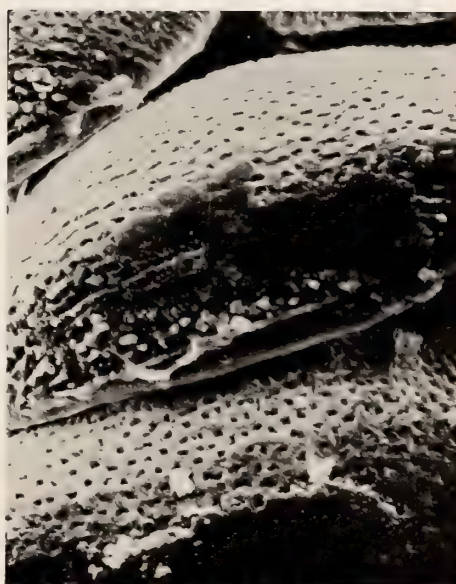


Figure 10

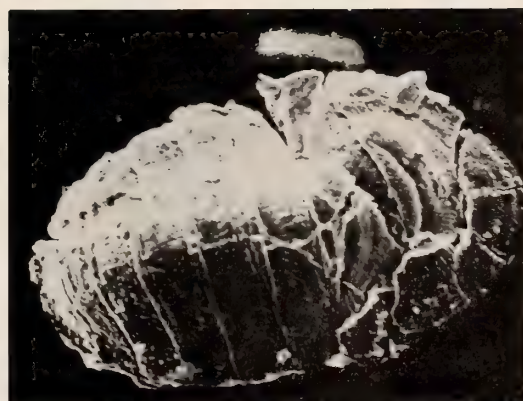
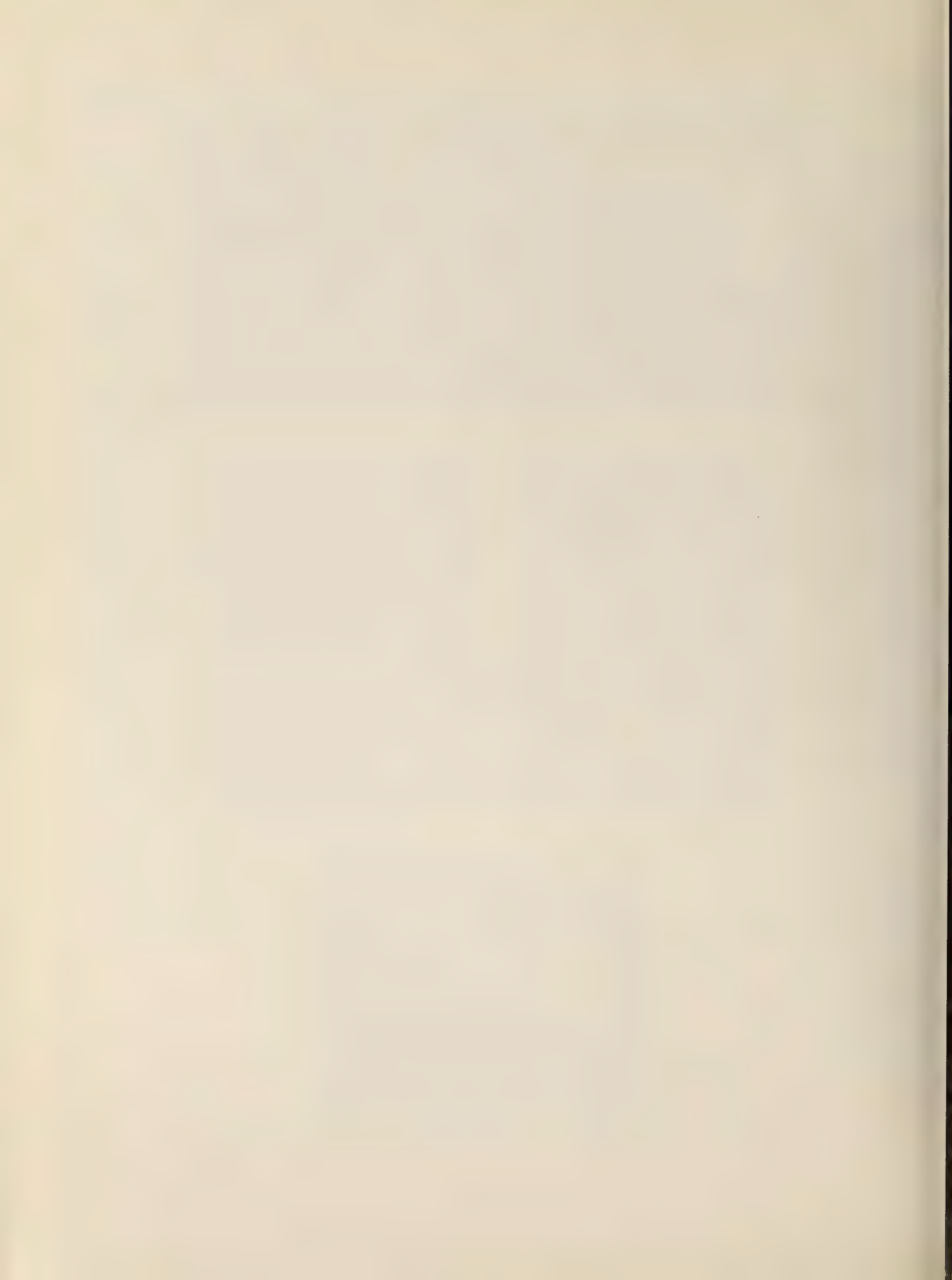


Figure 12



1958: 522; *Amphineura* fig. 27 - LINDSAY, 1966: 347 - THORPE in Keen, 1971: 873; *Polyplacophora*, fig. 28 - ABBOTT, 1974: 399 - A. G. SMITH & FERREIRA, 1977: 88
Callistochiton infortunatus PILSBRY, 1893, 14: 266; plt. 59, figs. 37-42 - DALL, 1909: 246 - PILSBRY & LOWE, 1932: 129 - STRONG, 1937: 194 - STEINBECK & RICKETTS, 1941: 552; plt. 27, fig. 2 - A. G. SMITH & GORDON, 1948: 208 - KEEN, 1958: 522; *Amphineura*, fig. 28 - LINDSAY, 1966: 347 - THORPE in Keen, 1971: 873; *Polyplacophora*, fig. 29 - ABBOTT, 1974: 399
Callistochiton decoratus infortunatus. DALL, 1921: 194 - OLDROYD, 1927: 896-897 - A. G. SMITH, 1947: 18
Callistochiton leidensis NIERSTRASZ, 1905: 143-145; plt. 9, figs. 2-10

Description: Roundly arched to subcarinated chitons. Length up to 2 cm. Color tan to rusty brown or dark green. Anterior valves with 8-10 well defined radial ribs separated by pitted spaces about as wide as the ribs; the radial ribs are somewhat triangular in cross-section, and often crowned by a series of 6-10 small knobs. Posterior valve rather variable in shape, from elevated and strongly convex to low and flat; mucro central; 7-10 radial ribs in the post-mucro area, usually not quite as well defined as those in the anterior valve. In the intermediate valves, the lateral areas are bicostate, the radial ribs with the same characteristics as in the anterior valve. Central area shows longitudinal riblets, 10-15 per side, finely latticed and with a tendency to diverge forward. The articulamentum is whitish to olivaceous, often with a dark brown discoloration at the apex of the end valves. Sutural plates subquadrate; sinus relatively narrow. Insertion teeth short and with festooned free edges. Slit formula 9-1-8. Eaves solid and narrow. Girdle often

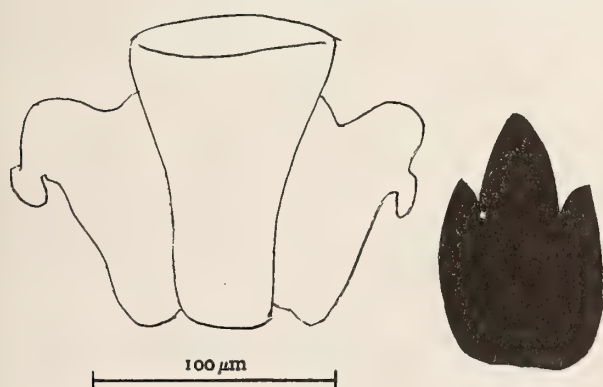


Figure 14

Callistochiton gabbi Pilsbry, 1893

Radula: Median tooth, first lateral teeth, and head of second lateral tooth. Specimen collected at Guaymas, Sonora, Mexico (LACM 64-4), original length 16.0 mm

banded, covered with oval imbricating scales, about 150 μ m in length, and with 12-15 fine striations (Figure 13).

The radula is figured here for the first time (Figure 14). The specimen (LACM 64-4, Guaymas, Sonora, Mexico, leg. J. H. McLean, 30 January to 2 February 1964, at 5-13 m), from a lot of 18 specimens, measures 16.0 mm in length. The radula is 5.2 mm long, that is 32% of the body length, and has 55 rows of mature teeth. The median tooth is larger in front where it measures 88 μ m in width, and has a small blade; the tooth narrows posteriorly to about 43 μ m. It is about 120 μ m long. The first lateral teeth are somewhat quadrangular, often showing a small knob at the outer-anterior corner. The second (major) lateral teeth have a tricuspid head which measures about 60 μ m in width, and 75 μ m in the length of its middle (longest) cusp. Outer marginal teeth are elongated, about 75 μ m long and 60 μ m wide.

Type Material: Holotype (ANSP 118691) (Figure 15).

Type Locality: "Gulf of California" (PILSBRY, 1893, 14: 270), here restricted to Puertecitos (30°20'N, 114°39'W), Baja California, Mexico.

Distribution: Throughout the Gulf of California, Mexico, to Ecuador. *Callistochiton gabbi* has been collected practically everywhere in the Gulf of California from San Felipe to Cabo de San Lucas, from Puerto Peñasco, Sonora to Mazatlan, Sinaloa, including Bahía de Concepcion, and islands of Tiburon, Angel de la Guarda, Carmen, Danzante, San José, Espíritu Santo, Cerralvo, and others. Although with less abundance, *C. gabbi* has also been found in southern Mexico, at Isla Isabella, Nayarit (LACM-AHF 19; LACM-AHF 124-33), Banderas Bay (LACM 71-83), Bahía Cuastocomate, Jalisco (LACM 68-41), Santiago Peninsula, Colimas (LACM 63-10), Zihuatanejo (AJF 305) and Acapulco, Guerrero (AJF 307); Puerto Escondido (AJF 300) and Puerto Angel, Oaxaca (AJF 302); and farther south, Bahía Herradura, Costa Rica (LACM 75-52), Taboga Island, Panama (LACM 65-25), and Punta Ancón, Santa Elena Peninsula [2°20'N, 80°53'W], Ecuador, its southernmost record (LACM 70-11 & 70-12, leg. J. H. McLean, 6-7 March 1970). Bathymetrically, *C. gabbi* has been found from low intertidal to "20-40 fathoms" [37-73 m] (LACM 38-5).

Remarks: PILSBRY (1893) described *Callistochiton gabbi* 4 pages after describing *C. infortunatus* "from Carpenter MSS and unpublished drawings of his types" in the Manual of Conchology.

While he attempted to distinguish *Callistochiton gabbi* from other similar species such as *C. decoratus*, *C. elenensis*, and even "Carpenter's unfigured *Ischnochiton ex-*

pressus," he failed to mention the extraordinary similarities between *C. gabbi* and *C. infortunatus*. Despite the awareness that both nominal species came from the same general locality, the Gulf of California and the Panamic province, Pilsbry's differential diagnosis was limited to the profile of the tail valve which he described as "convex, mucro obtuse" in *C. infortunatus*, and "rapidly sloping backward from the front margin, mucro flat" in *C. gabbi* (PILSBRY, 1893: 262; "Key to species of *Callistochiton*").

The examination of many lots of *Callistochiton* from the Gulf of California down to Central and South America has convinced me that Pilsbry's species-group names, *C. gabbi* and *C. infortunatus*, refer to the same zoological species. The alleged differences in tail-valve profile and mucro appeared highly unreliable for distinguishing the 2 forms inasmuch as there are many specimens showing intergradation, often collected side by side at the same station; and no other characters, such as color, tegmental sculpture, articulamentum, girdle scales, or radula correlated in any significant manner with either morph.

However, it is not without some justification that authors have adhered to, or at least left unquestioned Pilsbry's notion of 2 species. *Callistochiton gabbi* is given to considerable intraspecific variation in color, sharpness of sculptural features, number of radial ribs in the end-valves, and profile and mucro of the tail valve. In color, specimens from the Gulf of California tend to be drabby looking, tan to olive, whereas specimens from the southern part of the range tend to be much more colorful, sometimes in bright creamy browns, with reddish hues, even suffusions of cobalt-blue as was seen in a specimen from Taboga Island, Panama. In the number of ribs in the anterior valve, specimens from the Gulf of California tend to have 9 radial ribs (in a sample of 75 randomly selected specimens from the Gulf of California, 96% had 9 ribs in the anterior valve, 4% had 8), while specimens from southern locations tend to have 8 (in a sample of 16 specimens, 94% had 8, 6% had 9 ribs in the anterior valve). In both geographic populations the number of ribs in the posterior valve shows greater fluctuation. Of the samples mentioned, in the Gulf of California 10% of the specimens had 6 radial ribs, 30% had 7, 30% had 8, 25% had 9, and 6% had 10; while in the southern range 6% had 6, 62% had 7, 19% had 8, and 12% had 9 radial ribs. In the case of the profile and mucro of the tail valve a definition of the morphs "*infortunatus*" (elevated mucro, convex post-mucro) and "*gabbi*" (low mucro, flat post-mucro) was made difficult as there were many intergradations. Considering only the extreme cases, i. e., those specimens that clearly fit the definition "*gabbi*" or "*infortunatus*," it was a simple matter to

conclude that the morph "*gabbi*" was virtually confined to the Gulf of California, whereas the morph "*infortunatus*" was to be found throughout the range from the upper Gulf of California to Ecuador. In considering all the specimens available to me, there are many instances when the tail valve could not be so easily classified one way or the other, and all manners of intergradation of the mucro and the posterior valve's profile could be seen between the two extremes, "*infortunatus*" and "*gabbi*." Often, these extremes and intergradations were found in specimens from the same lot; for instance, a lot of 31 specimens from Saladita Cove, Guaymas, Sonora (LACM 68-27) contained 18 specimens that would be classified as "*gabbi*," 7 as "*infortunatus*," and 6 as "in between." In a lot of 16 from Puertecitos, Baja California (LACM 62-19) only about 2 or 3 specimens would fit a rigorous definition of "*gabbi*," 1 or 2 that of "*infortunatus*"; whereas the bulk of the lot, some 12 specimens, would have to be regarded as intermediates.

As first reviser, I have selected the name *Callistochiton gabbi* for the species. Despite the fact that *C. infortunatus* has page priority, the name *C. gabbi* has the advantage of an already assigned type specimen (there is none for *C. infortunatus*), and a less ambiguous type locality and description. The examination of the holotype of *C. gabbi* was made possible through the kindness of Dr. Robert Robertson, Curator, Academy of Natural Sciences, Philadelphia.

Callistochiton leidensis Nierstraß, 1905, described from a single specimen, 8mm long, collected at "Porta Santae Elenae" [? Ecuador] appears to be, from the description and figures, a synonym of *C. gabbi* as here defined.

Callistochiton colimensis (A. G. Smith, 1961)

(Figures 16, 17, 18)

Ischnochiton colimensis A. G. SMITH, 1961: 86-87; pl. 9, fig. 2

Callistochiton colimensis. THORPE in KEEN, 1971: 873; fig. 26
Ischnochiton lowei PILSBRY in PILSBRY & LOWE, 1932: 129 [nomen nudum]

Description: Oval, relatively high arched, somewhat carinated chitons (Figure 16). Length up to 2.5 cm. Color predominantly golden brown to cinnamon. Tegmental surface microgranular. Anterior valve with 11 - 13 strongly defined radial ribs, with a tendency to twin towards the periphery, crowned by minute, 100 μ m in diameter, round tubercles. Lateral areas of intermediate valves usually bicostate; however, in large specimens a sulcus

often appears in the rib dividing it radially. Radial ribs similar to those in anterior valve, crowned by minute tubercles, about 6 - 8 per rib. Central area has longitudinal riblets, about 10 per side, which remain parallel to the jugum or, as is more commonly the case, tend to converge somewhat forward. Riblets, separated by cross-ribbed spaces, become crowded towards the jugum. Jugal area longitudinally ribbed; there is no wedge-like figure on valve ii (such as seen in many species of *Lepidozona*). Mucro of posterior valve slightly but definitely anterior; post-mucro with 10 - 11 radial ribs similar to those in anterior valve. Girdle, sometimes faintly banded, is covered with closely imbricated oval scales, up to 240 μm in length, displaying 10 - 16 fine striations (Figure 17).

Articulamentum white. Sutural laminae semioval and sharp; sinus shallow. Insertion plates with relatively sharp teeth, vaguely thicker at the edges, but showing no festooning. Slit formula of paratype, 10 - 1 - 10; of another specimen examined, 9 - 1 - 9. Slits correspond in number and position to the tegmental ribs.

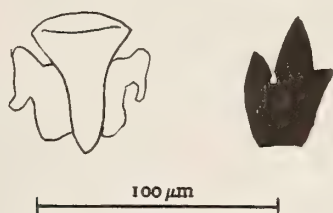


Figure 18

Callistochiton colimensis (A. G. Smith, 1961)

Radula: Median tooth, first lateral teeth, and head of second lateral tooth. Specimen collected in Gulf of Tehuantepec, Mexico (Don Shasky collection), original length 7.5 mm

The radula is figured here for the first time (Figure 18). In a specimen 7.5 mm long (Don Shasky Collection: "45 fathoms [82 m], rocky bottom, San Juan Exped., Gulf of Tehuantepec [Mexico], July 10, 1963, leg. Don Shasky"). the radula measures 2.75 mm in length, and has 46 rows of mature teeth. Relative length, 37%. Median tooth wider in front, where it measures about 50 μm in width, and bears a thin blade; posteriorly, it narrows rapidly to 25 μm , tapering to a point. In length it measures about 60 μm . The first lateral teeth are not easily visualized in this particular preparation; they are somewhat quadrangular, and slightly angulated at the outer-anterior corner. The second (major) lateral teeth have a tricuspid head, about 38 μm wide; the middle cusp, the longest, is about 50 μm

long. Of the other 2 cusps, the outer cusp is the larger; the inner cusp is small, hardly noticeable. Outer marginal teeth are somewhat elongated, about 53 μm long and 38 μm wide.

Type Material: Holotype (ANSP 152139); one paratype (CASG 12342).

Type Locality: "Manzanillo [19°03'N, 104°20'W], Colima, Mexico," collected by H. N. Lowe, 1930.

Distribution: *Callistochiton colimensis* is quite rare, although its geographic range known at present extends from 23°N to 8°N. Specimens from the following stations were examined: "Pinacle north of Pescadero Canyon [23°00', 109°35.7'W, its northernmost record], off San José del Cabo, inside Inner Gorda Bank," Gulf of California, Mexico, at 330 - 340 m (CASIZ, leg. R. H. Parker, R/V *Spencer F. Baird*, Vermillion Sea Expedition, 28 March 1959, 2 specimens); Los Arcos [20°40'N, 105°20'W], Banderas Bay, Jalisco, Mexico, at 5 - 24 m (LACM 65-15, leg. J. H. McLean & C. Miller, 22-24 March 1965, 1 specimen); Bahía Cuastocomate [19°14'N, 104°45'W], Jalisco, Mexico, 5 - 22 m (LACM 68-41, leg. H. J. McLean & Oringer, 13 - 21 October 1968, 5 specimens); Manzanillo [19°03'N, 104°20'W], Colima, Mexico, intertidal (CASG 12342, leg. H. N. Lowe, 1930, 2 specimens, type lot, only paratype examined); Gulf of Tehuantepec [15°08'N, 93°23'W], Mexico, 82 m (Don Shasky Collection, leg. D. Shasky, San Juan Expedition, Sta. N-13, 10 July 1963, 6 specimens); Port Parker [10°58'N, 85°49'W], Costa Rica, 9 m (LACM-AHF 468-35, 9 February 1965, 2 specimens); Bahía Elena [10°57'N, 85°46'W], Costa Rica, 26 - 53 m (LACM 72-12, leg. P. LaFollette & D. Cadien, R/V *Searcher*, Sta. 392, 14 February 1972, 2 specimens); Isla Contadora [8°38'N, 79°02'W], Archipiélago de las Perlas, Gulf of Panama, Panama, 2 - 6 m, (AJF 224, leg. A. J. & N. J. Ferreira, 17 - 19 February 1975, 1 specimen).

The bathymetric range of *Callistochiton colimensis* established by these collections extends from the intertidal zone to 330 - 340 m.

Remarks: The similarities between *Callistochiton colimensis* and *C. asthenes* are noteworthy: (1) the tegmentum has similar texture; (2) the end-valves and the lateral areas of the intermediate valves have about the same number of radial ribs; (3) the radial ribs are crowned by a series of minute tubercles; (4) the mucro is anterior; (5) the central areas have about the same number of latticed longitudinal riblets; (6) the girdle scales are about the same size and striated. Yet the 2 species are quite distinct: (1) in size, *C. colimensis* reaches

lengths 3 times that of *C. asthenes*; (2) much warmer and brighter color can be seen in *C. colimensis*; (3) the radial ribs are much better defined, more rounded, and stronger, with a tendency to twin in *C. colimensis*; (4) the longitudinal ribs and laticing of the central areas are boldly sculptured in *C. colimensis*, only faintly visible in *C. asthenes*; (5) at the jugum, the longitudinal riblets are crowded but clearly present in *C. colimensis*, while invariably absent in *C. asthenes*; and (6) the girdle scales have more and finer striations in *C. colimensis* than in *C. asthenes*, and the pitted appearance of the striae, characteristic of the latter, is not present in the former. Still, young specimens of *C. colimensis* look remarkably similar to *C. asthenes*, and the differential diagnosis based on a single such specimen may prove rather difficult. In view of these similarities, it seems probable that the 2 species, *C. colimensis* and *C. asthenes* are closely related and share a common ancestral line.

Callistochiton elenensis (Sowerby, 1832)

(Figures 19, 20, 21)

- Chiton elenensis* SOWERBY in Broderip & Sowerby, 1832: 27 - MÜLLER, 1836: 164 - SOWERBY, 1840: 6, sp. no. 79 [spelled "ellinensis"]; p. 10, fig. 69 - [?] REEVE, 1847: sp. no. 116; pl. 19, fig. 116 (syn. of *Chiton janeirensis* Gray, 1828) - CARPENTER, 1857: 180, 318
- Ischnochiton elenensis*. CARPENTER, 1864: 552 - 553 [reprinted, 1872: 38, 39]; 1865: 275 [reprinted, 1872: 266]
- Callistochiton elenensis*. HADDON, 1886: 20 - PILSBRY, 1893, 14: 267 - 268 - DALL, 1909: 246 - KEEN, 1958: 522 - FERREIRA, 1974: 175; 1976: 49
- Lepidozona elenensis*. THORPE in Keen, 1971: 871, Polyplacophora, fig. 33 (with syn. *Lepidopleurus clathratus* Carpenter, 1857, *Ischnochiton expressus* Carpenter 1865, and *I. subclathratus* Pilsbry, 1892)
- Callistochiton flavidus* THIELE, 1910: 87 - 88; pl. 9, figs. 14 to 17 - KEEN, 1958: 522; *Amphineura* fig. 26 - [?] RICH, 1971: 133, 141 - FERREIRA, 1974: 175
- Lepidozona flavida*. THORPE in Keen, 1971: 875; Polyplacophora, fig. 34

Ischnochiton expressus CARPENTER, 1864: 552 [reprinted, 1872: 38] (*nomen nudum*); 1865: 275 - 276 [reprinted, 1872: 266 - 267] - THORPE in Keen, 1971: 871 (syn. of *Lepidozona elenensis*)

Callistochiton expressus PILSBRY, 1893, 14: 268 - 269 - KEEN, 1958: 522

Description: Relatively high arched, and carinated chitons. Length up to 11 mm. Color tan to creamy brown, sometimes reddish or greenish. Anterior valve with 11 - 12 rounded to flattish ribs, in some specimens slightly granose; the ribs are more like undulations of the tegmentum than "added on" features, the space between the "ribs" being as wide as the ribs themselves. The lateral areas of the intermediate valves are well marked by the presence of 2 radial ribs, similar to those found in the anterior valve; the anterior rib of the lateral areas is usually quite smooth in appearance while the posterior rib is often granose conferring a serrated appearance to the sutural space. The central areas have about 10 longitudinal riblets per side, which tend to diverge forwardly and are cross-ribbed very weakly in most specimens. The jugal area is usually ribbed, too. The posterior part of the valves iv to vii, particularly the latter, have an upswept appearance which gives the specimen a peaked profile. The posterior valve has a central, rather flat mucro; post-mucro area is depressed, with 8 - 11 radial ribs very poorly defined. The girdle is covered by oval, imbricating scales, about 100 μ m in length, with some 20 ribs separated by deep striations (Figures 19, 20).

The articulamentum is whitish; often a brown discoloration may be seen at apex of valve viii. Sutural laminae are semioval and sharp; sinus quadrate. Insertion plates are cut into relatively sharp teeth; festooning is not obvious, but there seems to be some thickening of the edges of the teeth. Slit formula of a specimen 8.5 mm long (AJF 134, Masachapa, Nicaragua, leg. A. J. Ferreira, 23 January 1974) is 9 - 1 - 9.

Radula of the same specimen (Figure 21) measures 2.7 mm in length (relative length, 32%) and has some 30

Explanation of Figures 13, 15, 19, 20, 22, 23, 25

Figure 13: *Callistochiton gabbi* Pilsbry, 1893. Girdle scales.

SEM micrograph by Dennis Nichols and Myrl Stone $\times 100$

Figure 15: *Callistochiton gabbi*. Holotype (ANSP 118691)

Figures 19 and 20: *Callistochiton elenensis* (Sowerby, 1832).

Girdle scales. SEM micrographs by Hans Bertsch $\times 300$ and $\times 1000$, respectively

Figures 22 and 23: *Callistochiton periconis* Dall, 1908. Girdle scales. SEM micrographs by Hans Bertsch $\times 650$

Figure 25: *Callistochiton pulchellus* (Gray, 1828). Lectotype (BM(NH) 197739)

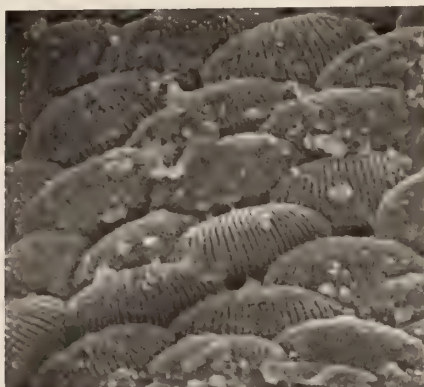


Figure 19



Figure 20



Figure 22



Figure 23

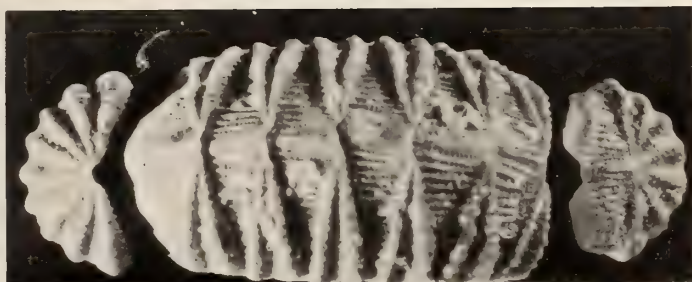


Figure 15

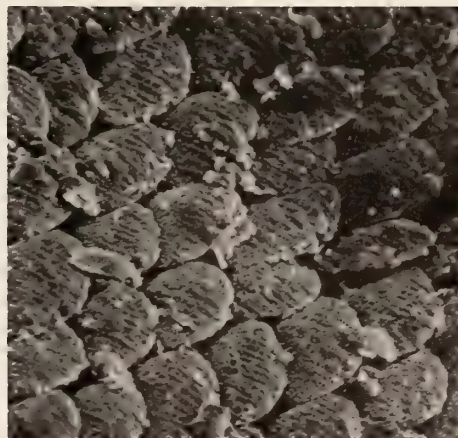


Figure 13



Figure 25



rows of mature teeth. The median tooth is wider anteriorly where it bears a thin blade, and measures $65\ \mu\text{m}$ in width; posteriorly, it narrows to $25\ \mu\text{m}$ and then enlarges into a bulb $35\ \mu\text{m}$ in diameter. In length it measures about $90\ \mu\text{m}$. The first lateral teeth are quadrangular with a knobby protuberance at the outer-anterior corner. The second (major) lateral teeth have a unicuspid head, measuring about $50\ \mu\text{m}$ in width, and $85\ \mu\text{m}$ in length. The outer marginal teeth are quite elongated, $75\ \mu\text{m}$ long and $38\ \mu\text{m}$ wide.

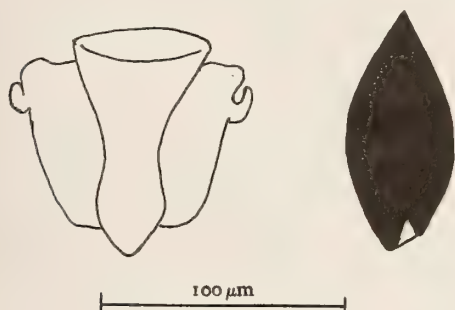


Figure 21

Callistochiton elenensis (Sowerby, 1832)

Radula: Median tooth, first lateral teeth, and head of second lateral tooth. Specimen collected at Massachapa, Nicaragua (AJF 134), original length 8.5 mm

Type Material: Sowerby's type material of *Chiton elenensis* is presumed lost or never designated. However, the species was illustrated, though poorly, by Sowerby in the Conchological Illustrations (fig. 69) [reprinted in PILSBRY, 1893, 14: plt. 59, figs. 27-28] and there seems to be no confusion in the current literature as to the zoological species involved. The "exceptional circumstances" for the naming of a neotype (ICZN, Article 75) do not seem to be present, and none is designated herein.

The whereabouts of Thiele's type material of *Callistochiton flavidus* is unknown; it was not found at the Museum of the Humboldt-Universität, Berlin (Dr. Rudolf Kilius, *in litt.*, 31 January 1977).

The type material of Carpenter's *Ischnochiton expressus*, if ever designated, could not be located at the U. S. National Museum of Natural History (Dr. J. Rosewater, *in litt.*, 24 March 1977) or at the Academy of Natural Sciences of Philadelphia (M. Miller, *in litt.*, 27 March 1978).

Type Locality: "St. Elena [?Ecuador] and Panama" (SOWERBY, 1832: 27).

Distribution: *Callistochiton elenensis* seems to have a continuous distribution between the parallels 23°N and 2°S . The northernmost record is Playa Cerrito [$23^{\circ}20'\text{N}$, $106^{\circ}30'\text{W}$], some 15 km N of Mazatlan, Sinaloa, Mexico (AJF 427, leg. A. J. & N. J. Ferreira, 7 July 1978, 6 specimens at 1-3 m). The southernmost record is Punta Ancón ($2^{\circ}20'\text{S}$, $80^{\circ}53.5'\text{W}$), Santa Elena Peninsula, Ecuador (LACM 70-12, leg. J. H. McLean, 7 March 1970, intertidally). Bathymetrically, the species ranges from the low intertidal zone to 18-90 m (CASG 23779).

Remarks: *Callistochiton elenensis* has a sibling species in the Caribbean, *C. portobelenensis* Ferreira, 1974, from which it differs by its (1) somewhat sharper tegmental features, (2) more angular and carinated appearance, (3) frequent presence of longitudinal riblets at the jugum, (4) "upswept" appearance of valves vi and vii, (5) thinner and more widely separated longitudinal riblets, and (6) ornamentation of the girdle scales [only evident in SEM micrographs, cf. Figures 19, 20 with FERREIRA 1974: figs. 3-5].

The synonymization of *Callistochiton flavidus* Thiele, 1910, is based upon the description and illustration of the species by Thiele. Although I have not been able to examine Thiele's type, it is quite clear that the specimen before him, a single specimen 6 mm long from Champerico [$14^{\circ}18'\text{N}$, $91^{\circ}55'\text{W}$], Guatemala, was a juvenile of *C. elenensis*.

The report of *Callistochiton flavidus* in Brazil (RIGHT, 1971) could not be verified; I consider it extremely doubtful, and most likely a misidentification.

The placing of *Callistochiton expressus* (Carpenter, 1865) in the synonymy of *C. elenensis* was already suggested by Carpenter himself when describing *Ischnochiton* (?var.) *expressus*, upon the examination of only 2 specimens, with the statement that they had "a strong general resemblance to *I. elenensis*" (CARPENTER, 1865: 276). Now, with more material available, and a fuller appreciation of the extent of intraspecific variation in *C. elenensis*, the conclusion of conspecificity becomes obvious.

On describing *Chiton elenensis*, SOWERBY (1832: 27) remarked: "This is the *Chiton Janeirensis*, var.?, Gray. It is unquestionably a distinct species, as Mr. Gray hints it may be, from his *Chit. Janeirensis*." Of course, Sowerby was correct in judging his *Chiton elenensis* to be distinct from *Chiton janeirensis* Gray, 1828 [type locality: Rio de Janeiro, Brazil]; but he was incorrect in considering *C. elenensis* conspecific with "*Chiton janeirensis* (var.?)

Gray, 1828" [type locality: Valparaiso, Chile]. Thanks to the generosity of Aileen Blake, Mollusca Section, Department of Zoology, British Museum (Natural History), I had the opportunity of examining the type material of the species in question. As reported elsewhere (FERREIRA, 1978b), the examination of the type specimens revealed that *Chiton janeirensis* Gray, 1828, from Rio de Janeiro is indeed distinct from "*Chiton janeirensis* (var.?)" Gray, 1828, from Valparaiso; while the former species retains its name as type species of the genus *Calloplax* Thiele, 1909, the latter, also a *Calloplax*, appeared to be conspecific with the later-named *Callistochiton viviparus* Plate, 1899.

Likely, on the strength of SOWERBY'S (1832) own statement that *Chiton elenensis* "is the *Chiton Janeirensis*, var.?, Gray", REEVE (1847) was also led into confusion and error. In the Monograph, having already described *Chiton janeirensis* Gray, "*Hab. Rio Janeiro*" (plt. 15, sp. 80), Reeve "discovered" and, as such, described what he believed to be the authentic *C. janeirensis*, "*Hab. Rio Janeiro. St. Elena, West Columbia [sic]; Cuming*" (op. cit.: plt. 19, sp. 116). Thus, he proposed the name *C. sowerbianus* [listed as species "80. Sowerbyi Reeve" in the "Detail of Sculpture" part of the Monograph] for the species first described (sp. 80), and relegated *Chiton elenensis* Sowerby to the synonymy of the *C. janeirensis* Gray (sp. 116) as later described.

The examination of the chiton specimens from the Cuming Collection that apparently caused Reeve to re-describe *Chiton janeirensis* proved to be of more than historical interest. Loaned for study through the generosity of Aileen Blake (BMNH), the lot consists of 5 specimens preserved dry and in good condition. The specimens, varying in length from 9.2 to 15.0 mm, are accompanied by a Museum label which reads: "B. M. (N. H.) reg. no.: / *Chiton janeirensis* Gray / FIGURED SPECIMEN / Rio Janeiro / H. CUMING colln. / 5 specs. Acc. no: 1829 / Conc. Icon. 4 *Chiton* / pl. XIX sp. 116 fig. 116, / (fig. = largest spec.), / Reeve." On the face of the wooden tablet underneath the glued specimens, is handwritten in ink: "*Leptochiton Janeirensis* Gray / Rio Janeiro: St. Elena." Examination of the specimens on the tablet reveals that 4 of them, including the figured one, conform in all respects to the present concept of *Calloplax janeirensis* (Gray, 1828); however, the remaining specimen, the smallest of the lot (9.2 mm in length) is not *C. janeirensis* but *Calloplax vivipara* (Plate, 1902) [type locality, Urica, Chile; see FERREIRA, 1978], a species which, if girdle characteristics are disregarded, does resemble *Chiton elenensis* Sowerby.

Callistochiton periconis Dall, 1908

(Figures 22, 23, 24)

- Callistochiton periconis* DALL, 1908: 355-356 - KEEN, 1958: 522 - THORPE in Keen, 1971: 873 (syn. of *C. pulchellus* (Gray, 1828)) - A. G. SMITH, 1977: 217, 242-243 (syn. of *C. pulchellus* (Gray, 1828))
- "*Chiton pulchellus* Gray" - C. B. ADAMS, 1852: 243 - CARPENTER, 1857: 277; 1864a: 362 [reprinted, 1872: 198]; 1864b: 552 [reprinted, 1872: 38] [not *Chiton pulchellus* Gray, 1828]
- "*Chiton (Callochiton) pulchellus* Gray." MÖRCH, 1861: 176 [not *Chiton pulchellus* Gray, 1828]
- "*Callochiton pulchellus*: diagn. auct." CARPENTER, 1857: 317; 1865: 276 [reprinted, 1872: 267] [not *Chiton pulchellus* Gray, 1828]
- "*Callistochiton pulchellus* (Gray)." PILSBRY, 1893, 14: 271 to 273; plt. 60, figs. 1-6 - NIERSTRASZ, 1905: 148; plt. 10, fig. 18 - PILSBRY & LOWE, 1932: 129 - KEEN, 1958: 522; Amphineura, fig. 30 (with syn. *Chiton bicostatus* Orbigny, 1841) - THORPE in Keen, 1971: 873; Polyplacophora, fig. 30 (with syn. *Chiton bicostatus* Orbigny, 1841; *Callistochiton periconis* Dall, 1908; *C. fisheri* Dall, 1919) - A. G. SMITH & FERREIRA, 1977: 88 [not *Chiton pulchellus* Gray, 1828]
- Callistochiton fisheri* DALL, 1919: 512; 1921: 194 - OLDROYD, 1927: 899 - LAROCQUE, 1953: 12 - THORPE in Keen, 1971: 873 (syn. of *Callistochiton pulchellus*) - ABBOTT, 1974: 399 - A. G. SMITH, 1977: 217, 241 (syn. of *C. pulchellus*)

Nomenclatural Comments: This common Central America species has been referred to as *Chiton pulchellus* Gray, 1828, by authors following C. B. ADAMS (1852), MÖRCH (1861), and PILSBRY (1893). The examination of Gray's type specimens of *Chiton pulchellus* (BMNH 197739) has conclusively demonstrated that Gray's original material, collected at Arica, Chile, is distinctly different from Central American "*pulchellus*."

The first available name for the Central American species is *Callistochiton periconis* Dall, 1908. It is a tribute to Dall that, with the description of *C. periconis*, he was the first author to realize that the Central American species differed from *C. pulchellus* (Gray) in several important particulars. Unfortunately, under the lasting influence of Pilsbry's Manual, Dall's observations were ignored and *C. periconis* relegated to the synonymy of the erroneously called "*pulchellus*." In this respect, it is interesting to note that even LELOUP (1953), having examined Gray's syntypes at the British Museum (Natural History), did not notice the discrepancies involved as he spoke of "this species . . . well described and figured by Pilsbry (op. cit.: 19).

Original Description: "Animal small, of a pale brownish color with a narrow dark girdle covered with small, closely packed setose scales; middle valves with the sculpture of *C. pulchellus* (Gray) Pilsbry, from Peru, but differing in the following particulars: the posterior ribs of the middle valves are transversely striated, not nodular, and do not serrate the suture; the anterior valve has thirteen rounded finely cross-striated ribs, the posterior has seven; this valve considerably overhangs the posterior part of the girdle, and the two anterior ribs are conspicuously larger and stronger than the five between them. The gills are prolonged, reaching the second valve. Perico Island, Panama Bay, collected on the reefs by the 'Albatross' party, U. S. N. Mus. 110,763." (DALL, 1908: 355-356).

Expanded Description:

High arched, round backed chitons, up to 1.5 cm in length. Color buff-cream to very dark brown. Anterior valve with 10-13 strong rounded radial ribs, often cut by a vague series of concentric transverse growth lines. Posterior valve elevated, with a mucro markedly posterior; post-mucro area strongly convex with 6-8 rounded radial ribs similar to those in anterior valve. Intermediate valves with elevated lateral areas bearing 2 prominent radial ribs of which the posterior is usually wider, and sculptured with transverse tubercles that, in some specimens, confer a serrated appearance to the sutural spaces. Central areas with longitudinal riblets that become diagonal and criss-cross, particularly in the midline, to form diamond-shaped pits. Girdle covered with strongly imbricating, oval scales, about 120 μ m long; although under ordinary magnifications appearing smooth, the surface of the girdle scales, when examined in SEM micrographs, is seen to be covered by minute spherules (often eroded away) on the upper face, and vertical ribs on the lateral faces (Figures 22, 23).

Articulamentum white, often with a bluish tint particularly accentuated in valve viii. Sutural laminae semioval, becoming quadrate in valves vii and viii. Sinus wide and shallow, often minutely notched. Insertion plate cut into strong teeth; in the posterior valve, the insertion plate is not prominent (the teeth tending to point away from the midline) and exhibits minute denticulations, irregularly disposed, inwardly. The massive thickness of the posterior valve makes its insertion plate, particularly in large specimens, less than conspicuous. The insertion teeth are often thickened at the edges and festooned, corresponding in position and number to the ribs of the tegmentum, except in larger specimens where often the number of teeth exceeds the number of tegmental ribs. In one of the specimens examined (AJF 218, Mensabé,

Panama, *leg.*, A. J. Ferreira, 12 February 1975, intertidal), 12.5 mm long, the slit formula is 10-1-11.

The radula of this specimen is 3.8 mm long (30% of the specimen's length), and comprises about 80 rows of mature teeth. The median tooth is slightly enlarged anteriorly where it bears a small blade, and measures about 28 μ m in width; from there it narrows slightly posteriorly, and then enlarges again to a width of about 30 μ m. In length, the tooth measures about 65 μ m. The first lateral teeth are subquadrate, about 80 μ m long, 25 μ m wide; they bear a small blade anteriorly. The second (major) lateral teeth have a long, bicuspid head; the outer cusp, the longer and larger, is about 80 μ m long and 25 μ m wide, while the inner cusp is much shorter and inconspicuous. The outer marginal teeth are squarish, measuring about 50 μ m in length and in width. The radula of *Callistochiton periconis* is figured here for the first time (Figure 24).

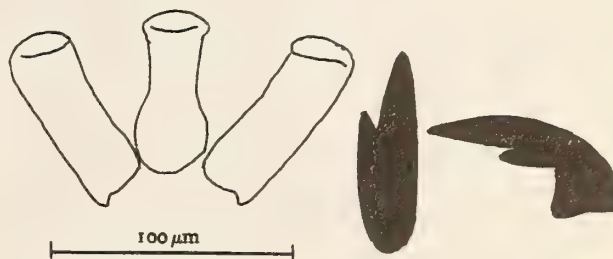


Figure 24

Callistochiton periconis Dall, 1908

Radula: Median tooth, first lateral teeth, and heads (dorsal and profile views) of second lateral teeth. Specimen collected at Mensabé, Panama (AJF 218), original length 12.5 mm

Type Material: Holotype (USNM 110763); color slide, photograph of the specimen taken by A. G. Smith, at CASIZ Color Slide Series no. 1927.

Callistochiton fisheri Dall, 1919: 6 syntypes (USNM 110353); color photograph of 4 of the specimens taken by A. G. Smith, at CASIZ Color Slide Series no. 1933.

Type Locality: Perico Island [8°55'N, 79°31'W], Panama Bay, Panama.

Distribution: The range of *Callistochiton periconis* is relatively narrow, extending only between parallels 11°N and 6°N. The northernmost record of the species is a small bay at "Hacienda Nacascolo," 2 km N of San Juan del Sur (11°15'N, 85°52'W), Nicaragua (AJF 138, *leg.*,

A. J. & N. J. Ferreira, low intertidal zone, 26 January 1974). The southernmost record is Punta Cruces ($6^{\circ}40'N$, $77^{\circ}33'W$), Colombia (CASIZ 006297, *leg.*, D. P. Abbott, *Te Vega* Cruise 18, sta. JT-20, intertidal, 2 May 1968), with many stations in between. The bathymetric range extends from the intertidal zone to 30 fathoms [55 m] (AJF Collection, Bahía Santa Elena, Costa Rica, R/V *Searcher*, Sta. 391 trawling, *leg.* A. J. Ferreira, February 1972). The largest specimen of *C. periconis* examined is 14.5 mm long, including girdle (ANSP 243632, reef at San Francisco, near Panama [City], *leg.*, Pilsbry, 17 May 1929).

Remarks: The placing of *Callistochiton fisheri* in the synonymy of *C. periconis* is based upon the observations of A. G. SMITH (1977) who examined and photographed the 6 specimens in the syntype series. The study of the color slides of 4 of the syntypes shows conclusively that *C. fisheri* and *C. periconis* are conspecific. As pointed out by A. G. SMITH (*op. cit.*: 241), the statement that *C. fisheri* had been collected in the Aleutian Islands must be considered as erroneous.

Callistochiton pulchellus (Gray, 1828)

(Figures 25, 26)

- Chiton pulchellus* GRAY, 1828: 6 (reference is made to plt. 3, fig. 9, never published but on file at BM[NH], *teste* A. Blake, in litt. 28 November, 1977) [not *Chiton pulchellus* Philippi, 1844] - REEVE, 1847: sp. 153, plt. 23, fig. 153 - PAETEL, 1873: 80
- Callochiton pulchellus*. H. & A. ADAMS, 1858: 471
- Callistochiton pulchellus*. DALL, 1909: 246 - BOUDET, 1945: 134 - LELOUP, 1953: 18-19; fig. 3 [misinterpreted]; 1956: 46 - STUARDO, 1959: 144, 146
- [Not *Callistochiton pulchellus ex auctore* treating Panamic specimens]
- Chiton bicostatus* ORBIGNY, 1841: 486; plt. 81; figs. 7-9; 1854: 54
- Callistochiton carmenae* A. G. SMITH & FERREIRA, 1977: 87 to 88; figs. 10-11
- Callistochiton shuttleworthianus* Pilsbry. BERGENHAYN, 1936: 284-285; text figs. 3f-3g - KAAS, 1972: 100-101 - GÖTTING, 1973: 253 [not *C. shuttleworthianus* Pilsbry, 1893]

Original Description: "6. *Chiton pulchellus*, n. — *Testa oblonga, elongata, subcarinata, albido-lutescente; area centrali punctulata, laterali costis duobus latis, rugulosis; valvis terminalibus inaequaliter radiatim costatis*. Icon. t. 3.f.g. Inhab. Arica, Peru, Rev. W. Hennah. Brit. Mus. Shell oblong, elongate, slightly keeled, yellowish white; end valves distantly unequally radiately ribbed; lateral

area of the middle valves with two broad regular ribs; central area closely and deeply punctured. Margin yellowish white, with very minute bran-like scales. The ribs of the lateral areae are rarely bifid. Length $\frac{3}{8}$, breadth $\frac{1}{6}$ of an inch." (GRAY, 1828: 6).

As mentioned before, plate 3 of *Spicilegium Zoologicum* was not published. However, thanks to the generosity of Aileen Blake, Mollusca Section, Department of Zoology, British Museum (Natural History), I was able to study a xerox copy of that unpublished plate in the repository of the British Museum, and verified figure 9 as corresponding to Gray's description, above as well as to the syntype series (BMNH 197739).

Detail figure of the posterior valves is given by REEVE (1847: sp. no. 153). Both Gray's figure and Reeve's enlarged detail are reproduced by PILSBRY (1893) in plt. 60 as figs. 1 and 2, respectively.

Description: The type material (BMNH 197739) was examined on a loan secured through the kindness of Aileen Blake (BMNH), October 1977. The vial contains a single label which reads: "British Museum (Natural History) / *Chiton pulchellus* Gray / Syntypes / Reg. No. 197739 / 3 specs." An invoice accompanying the specimens states further, "Arica, Peru, Rev. Hennah."

The syntype series consists of 3 specimens, dry, flat, in fairly good condition; they show vestiges of glue and paper to which they were probably attached in the past. All 3 specimens are a uniform tan color, and show a diffuse black smudge along the jugum, obviously externally acquired. The specimens measure, including the girdle, 8.7×5.3 mm; 8.4×5.0 mm; and 6.6×3.5 mm. The largest specimen (Figure 25) here designated as **lectotype**, shows about 15 radial rows in the anterior valve; these ribs are very low in profile. The posterior valve has a central mucro, low, but slightly pointed; the post-mucro area is flat to slightly concave, showing some 11 radial ribs, low and weakly defined. The intermediate valves are subcarinated. The lateral areas are well defined; they bear 2 relatively flat radial ribs, the posterior rib weakly but definitely crenulated. The central areas are pitted; the pits are mostly round, and become much less accentuated, almost obsolete at the jugum. The girdle is covered with very small, seemingly striated scales. The 2 **paralectotypes**, although smaller in size, have virtually the same characteristic as the lectotype.

Among the chiton material collected in Chile by Dr. James H. McLean, 1975, 2 lots of *Callistochiton pulchellus* (Gray, 1828) were recognized. One (LACM 75-10) consists of 26 specimens, preserved in alcohol, bearing the locality label "Intertidal, Pozo Toyo (S of Iquique), Tarapaca Prov., Chile ($20^{\circ}25'S$, $70^{\circ}10.5'W$), *leg.* J. H.

McLean (sta. 1), 29 Sept., 1 Oct. 1975;" the other (LACM 75-12), consists of a single specimen, with the label "Intertidal, Iquique, marine lab. Universidad del Norte, Tarapaca Prov., Chile, (20°15.5'S, 70°08'W), leg. J. H. McLean (sta. 3), 30 Sept., 2 Oct., 1975." Thanks to the generosity of Dr. James H. McLean, Curator, Mollusks, Natural History Museum of Los Angeles County, I was permitted to study these specimens, and so add to the understanding of *C. pulchellus*.

The specimens examined are all rather uniform in color, creamy white, and in size. The longest specimen (LACM 75-12) measures 10.2 mm in length, the smallest, 5.6 mm. The mean size of all specimens studied (a total of 30, including the syntypes) is 7.7 mm in length. The number of radial ribs in the anterior valve is 12 in most specimens, although varying from 10 to 13; in the posterior valve the number of ribs is 8-10. In the lateral areas there are always 2 radial ribs. In most specimens the radial ribs are rather low and weakly defined, particularly in the post-mucro area of the posterior valve. The mucro of valve viii is clearly central in all specimens, and the post-mucro flat to concave. The central areas have round pits, as if made by the intercrossing of virtual diagonal riblets; the pits are deeper on the sides than in the jugal area. Actually, in most specimens, all tegmental features, the radial ribs, and the pitted central areas, are rather subdued, even subobsolete in some specimens.

The girdle scales are oval, about 120 μ m long and 40 μ m high. They show about 20 vertical rib-like formations on the lateral surfaces which define that many striae in between, and minute spherical globules on the upper surfaces. The girdle scales are well figured by LÉLOUP (1953: fig. 3) apparently from material obtained from the syntype specimens. The underside of the girdle is covered by rectangular, overlapping scales, featureless, measuring about 50 μ m by 10 μ m.

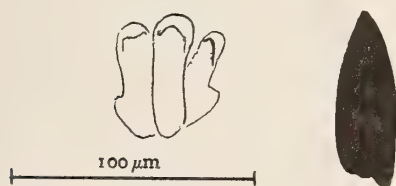


Figure 26

Callistochiton pulchellus (Gray, 1828)

Radula: Median tooth, first lateral teeth, and head of second lateral tooth. Specimen collected at Pozo Toyo, Chile (LACM 75-10), original length 7.0 mm

The radula of a specimen 7.0 mm long (LACM 75-10, Pozo Toyo, Chile) measures 2.3 mm in length, that is, 33%. It has about 46 rows of mature teeth. The median tooth is quite small (Figure 26), about 15 μ m wide, ending anteriorly by a rather round edge with a small blade. The first lateral teeth, difficult to see, seem to end anteriorly by a similar round edge. The second (major) lateral teeth have a unicuspid head, about 65 μ m long and 25 μ m wide; the inner aspect of the shaft, just below the head, bears a long protuberance, 20 by 8 μ m, pointing inwardly and anteriorly, obviously very fragile. The outer marginal teeth are 45 μ m long and 25 μ m wide.

The slit formula of this specimen is 9 - 1 - 10. Insertion teeth correspond in position to the ribs of the tegmentum. Gills abanal, about 18 plumes per side, extend to about 80% of the foot, becoming progressively larger posteriorly.

Type Material: Syntypes (BMNH 197739), 3 specimens, the largest designated lectotype herein. With the kind permission of the Trustees of the British Museum (Natural History), a photograph of Gray's specimen is published [© Trustees, BM(NH)] here for the first time (Figure 25).

Callistochiton carmenae A. G. Smith & Ferreira, 1977: Holotype (CASIZ, Type Series no. 696); paratypes (CASIZ Type Series no. 58248, and in the private collection of G. & L. Burghardt).

Type Locality: "Arica [18°29'S, 70°20'W], Peru [Chile]" (GRAY, 1828: 6).

Distribution: *Callistochiton carmenae* A. G. Smith & Ferreira, 1977, is here regarded conspecific with *C. pulchellus* (Gray, 1828). Thus, the distribution of *C. pulchellus* is known from 4 localities, 3 on the mainland (Arica, Pozo Toyo, and Iquique, in Chile), and the Galápagos Islands (about 0°30'S, 90°30'W), Ecuador. Probably better collecting along the west coast of South America will produce new collecting sites, and a clearer view of the distribution of the species. However, *C. pulchellus* does seem to be far from abundant. DALL (1909: 246) indicates he examined specimen(s) collected at Islay [17°03'S, 72°08'W], Chile. But LÉLOUP (1956) did not find the species among the collections obtained during the Lund University Chile Expedition, 1948-1949; and MARINCOVICH (1973) does not report the presence of *C. pulchellus* at Iquique, Chile. So, for the present *C. pulchellus*' southernmost record is Pozo Toyo (20°25'S); its northernmost record is the Galápagos Islands, and on the mainland, Islay (17°03'S).

Bathymetrically, *Callistochiton pulchellus* is known only from the intertidal zone.

Remarks: In addition to the type material, another lot of *Callistochiton carmenae* has come to my attention: It consists of 6 specimens, averaging 7.8 mm in length, collected 42 January 1938, intertidally, at Black Beach ($1^{\circ} 16' 26''\text{S}$, $90^{\circ} 29' 42''\text{W}$), Charles Island, Galápagos, Ecuador (LACM-AHF 806-38). Upon the realization of the true nature of *C. pulchellus* (Gray, 1828), a side by side comparison led to the conclusion that *C. carmenae* and *C. pulchellus* were conspecific. In all respects of significance — color, size, tegmental features, articulamentum, girdle scales, radula — the *C. carmenae* from the Galápagos is identical with the *C. pulchellus* from the mainland. The only noticeable distinction between the 2 geographic populations, albeit so far a constant one, lies in the much sharper tegmental features of *C. carmenae* when compared with *C. pulchellus*: The radial ribs of the anterior and posterior valves, as well as those from the lateral areas, and the pitted appearance of the central areas of the intermediate valves, are much more strongly defined, more incisedly sculptured in the Galápagos than in the mainland populations. Such sole distinction is, in my opinion, of less than specific significance. Conceivably, the Galápagos population of *C. pulchellus* could be considered distinct enough to warrant the name *carmenae* to be retained with subspecific rank; yet, I find it more satisfactory to regard those differences in the intensity of the tegmental sculpture as an expression of geographic variation, and relegate the nominal *C. carmenae* to the synonymy of *C. pulchellus*.

DISCUSSION

In the Eastern Pacific, 10 species of *Callistochiton* are here recognized, 5 in the north temperate region, 4 in the tropical region, and 1 in the south temperate region. Their distribution, illustrated in Diagram 1, demonstrates the faunal break known to exist at about Magdalena Bay ($24^{\circ} 30'\text{N}$) on the outer coast of Baja California, Mexico. As it had been found for *Lepidozona* species (FERREIRA, 1978), not a single species of *Callistochiton* crosses that barrier in either direction. Another faunistic break is demonstrated at the southern boundary of the tropical region. The only species of *Callistochiton* in the south temperate region, *C. pulchellus*, is recorded in the Galápagos Islands which, under the influence of the Humboldt Current may be regarded as an extension of the warm temperate region.

The taxonomic position of other nominal species of "*Callistochiton*" from the Eastern Pacific appears as follows: *Callistochiton aepynotus* Dall, 1919 has been shown

to be a synonym of *Mopalia sinuata* Carpenter, 1864 (A. G. SMITH, 1977). *Callistochiton duncanus* Dall, 1919 has been assigned to the genus *Calloplax* Thiele, 1909 (A. G. SMITH & FERREIRA, 1977); and so has *Callistochiton viviparus* Plate, 1899 (FERREIRA, 1978b).

Callistochiton shuttleworthianus Pilsbry, 1893 had been reported from Isla Floreana, Galápagos Islands, Ecuador, by BERGENHAYN (1937); the study of Bergenhayn's single specimen, available through the courtesy of Dr. Tor A. Bakke, Zoological Museum of Oslo, Norway, clarified the questionable identification (A. G. SMITH & FERREIRA, 1977). Bergenhayn's Galápagos specimen is to be referred to *Callistochiton pulchellus* (Gray, 1828).

The genus *Callistochiton* has a world-wide distribution, although nowhere is it represented by as many species as in the Eastern Pacific. In the Western Atlantic only 2

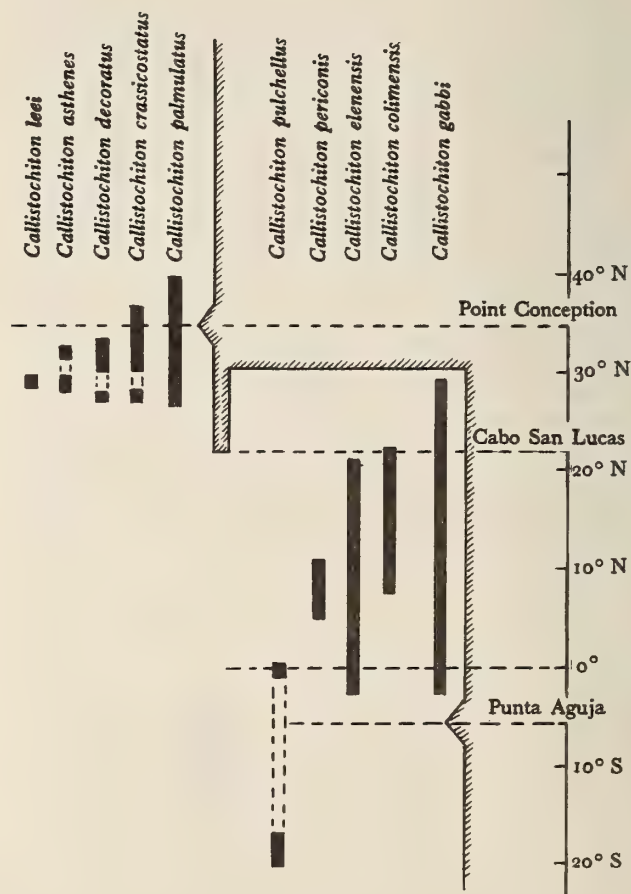


Figure 27

Geographical Distribution of the Species of *Callistochiton* Dall, 1879 in the Eastern Pacific

species of *Callistochiton* are known, *C. shuttleworthianus* Pilsbry, 1893 and *C. portobelensis* Ferreira, 1976. Judging from the description and illustrations, *C. incurvatus* Leloup, 1953 (type locality, "près de Pernambouc") is a junior synonym of *Ischnochiton pectinatus* (Sowerby, 1840), as already noted by RIGHI (1967) who nevertheless, ignoring the distinctly different characteristics of the girdle scales, preferred to assign the species to *Callistochiton* (RIGHI, 1967, 1971).

In the Eastern Atlantic no species of *Callistochiton* have been reported. SABELLI (1971) pointed out that *Chiton pachylasmae* Monterosato, 1879, allegedly collected in the Strait of Messina, Mediterranean Sea, does properly belong to *Callistochiton*. Examination of photographs of the single specimen of *C. pachylasmae* in the repository of the Museo Zoologico di Roma, kindly sent to me by Dr. Sabelli, Istituto di Zoologia, Università di Bologna, confirms the appropriateness of its assignment to *Callistochiton*. But the locality of *C. pachylasmae* remains in serious doubt in view of the fact that there seems to be no record of its having been collected again in the Mediterranean or elsewhere (Dr. B. Sabelli, *in litt.* 10 January 1977).

Although I have had no opportunity to study the several other species of "*Callistochiton*" described from elsewhere in the world, judging from their illustrations or descriptions, or both, it seems reasonable to accept the validity of the following: *Callistochiton jacobaeus* (Gould, 1859), in Japan; *C. adenensis* (E. A. Smith, 1891), in the Red Sea;

C. antiquus (Reeve, 1847), in South Australia; *C. granifer* Hull, 1923, in Australia (Queensland) and New Caledonia; *C. indicus* Leloup, 1953, in the Chagos Archipelago, Indian Ocean; *C. carpenteri* Nierstraß, 1905, Rio de Janeiro, Brazil; *C. madagassicus* Thiele, 1910 [= *C. adenensis* (E. A. Smith, 1891)], from Madagascar; *C. philippinarum* Thiele, 1910, in the Philippines.

A comparison of the characteristics of the different species of *Callistochiton* in the Eastern Pacific permits some observations regarding the girdle scales and the radula. All species of *Callistochiton* in the Eastern Pacific have relatively small girdle scales, rarely exceeding 150 to 200 μ m in length. In their shape and ornamentations, however, 3 basic morphologies appear: (1) striated scales, in which the striations would more properly be called steep undulations of the scale surface (*C. palmulatus*, *C. crassicosatus*, *C. decoratus*, *C. asthenes*, *C. gabbi*, and *C. colimensis*); (2) microgranular and smooth surfaced scales (*C. leei*); and (3) laterally ribbed scales with spherules on the upper surface (*C. pulchellus* and *C. periconis*), or without spherules (*C. elenensis*).

The taxonomic value of the radula in chitons is still a matter of controversy. Although it is clear now that in chitons radular characteristics are not species-specific, there is every indication that its careful study will prove useful to the understanding of the species and their possible relationships. Thus, it is informative to compare some relevant characteristics in the radula of *Callistochiton* in the Eastern Pacific (Table 1).

Table 1

Meristic characteristics of the radula of species of *Callistochiton* Dall, 1879, in the eastern Pacific.

Species	Length of spm. mm	Radula						
		relative length %	rows of teeth no.	median tooth width μ m	major lateral cusps no.	outer-marginal teeth		
						length μ m	width μ m	length/width ratio
<i>Callistochiton</i>								
<i>palmulatus</i>	16.2	39	40	95	2	115	75	1.5
<i>crassicosatus</i>	8.0	35	48	125	2	140	100	1.4
<i>decoratus</i>	21.0	32	70	100	2	100	80	1.3
<i>asthenes</i>	7.6	36	36	58	2	75	45	1.7
<i>leei</i>	8.1	34	80	37	3	35	25	1.4
<i>gabbi</i>	16.0	32	55	88	3	75	60	1.3
<i>colimensis</i>	7.5	37	46	50	3	53	38	1.4
<i>elenensis</i>	8.5	32	30	65	1	75	38	2.0
<i>periconis</i>	12.5	31	80	28	2	50	50	1.0
<i>pulchellus</i>	7.0	33	46	15	1	45	25	1.8

As far as the length of the radula is concerned, no essential differences were found among the species in question: All species had a radula with about the same relative length, that is between 31% and 39% of the specimen length, a difference which, considering the smallness of the sample cannot be regarded as significant.

The counting of the number of rows of "mature teeth" elicited some interesting differences among species: Although the number of rows cannot be taken literally since the human error in counting "mature rows" is considerable (perhaps as high as 10%), it came to light that certain species (*Callistochiton periconis*, *C. leei*) have a much larger number of rows (and consequently much shorter outer marginal teeth) than others (*C. elenensis*, *C. asthenes*).

As to the median tooth of the radula, the majority of the species have the same kind of tooth, enlarged anteriorly where it bears a sharp blade, and tapering posteriorly (*Callistochiton palmulatus*, *C. crassicosatus*, *C. decoratus*, *C. asthenes*, *C. gabbi*, and *C. elenensis*); but in *C. leei* the median tooth is quadrangular, and in *C. pulchellus* and *C. periconis* it is rectangular and elongated. The median tooth varies in the width of the anterior blade from 125 μ m in *C. crassicosatus*, to only 15 μ m in *C. pulchellus*, and 28 μ m in *C. periconis*.

The first lateral teeth in all specimens examined are very difficult to visualize. Here more than anywhere else in the study of the chiton radula, we wish for the day when SEM micrographs could be easily obtainable. In most of the species, the first lateral tooth is somewhat quadrangular with a knobby protuberance in the anterior-outer corner [the same morphology found in *Lepidozona* which, together with the very similar median tooth, likely accounted for THIELE's (1929) treatment of the 2 groups as subgenera of *Lorica*]. Such first lateral teeth are found in *Callistochiton palmulatus*, *C. crassicosatus*, *C. decoratus*, *C. asthenes*, *C. gabbi*, and *C. elenensis*, although the knobby formation at the anterior-outer corner is not always as conspicuous.

The second (major) lateral teeth in the *Callistochiton* of the Eastern Pacific have a head which may be (1) unicuspid (*C. elenensis*, *C. periconis*, and *C. pulchellus*); (2) bicuspid (*C. palmulatus*, *C. crassicosatus*, *C. decoratus*, and *C. asthenes*), or (3) tricuspid (*C. leei*, *C. gabbi*, and *C. colimensis*).

Lastly, the outer-marginal teeth whose significance in the study of the chiton radula has not been hitherto fully appreciated, show considerable variation from species to species. Two extremes may be distinguished: (1) Species with markedly elongated, *i. e.*, near twice as long as

wide, outer-marginals (*Callistochiton elenensis*, *C. pulchellus*, and *C. asthenes*), and (2) species with squarish, *i. e.*, length nearly as great as width, outer-marginals (*C. periconis*).

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A New Panamic *Mitrella*

(Mollusca : Gastropoda)

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(1 Plate)

ON ONE LOW TIDE series, from January 27, to February 2, 1975, William and Lois Pitt sampled the intertidal molluscan fauna in the vicinity of Puntarenas, Puntarenas Province, Costa Rica. On January 29 and 30, 1975, they sampled the fauna at Punta Coralillo, Bahía de Caldera. The substrate was rocky rubble above, and muddy sand below the mean low tide line. Prominent members of the molluscan fauna included *Fissurella* (*Cremides*) *virescens* Sowerby, 1835; *Scurria mesoleuca* (Menke, 1851); *Tegula* (*Agathistoma*) *verrucosa* McLean, 1970; *Thais* (*Vasula*) *melones* (Duclos, 1832); *Acanthina brevidentata* (Wood, 1828); *Cantharus* (*Gemophos*) *gemmatus* (Reeve, 1846); and *Anachis* (*Costoanachis*) *fluctuata* (Sowerby, 1832). Also occurring in abundance was a new species of *Mitrella* that is described herein. The animals were found aggregated on the undersides of rocks near the mean low tide line. A deep water port is under construction adjacent to the type locality. There will be a breakwater about 2 km to the north, angling from the shore of Bahía de Caldera in a northwesterly direction. Although the type locality will not be within the completed harbor, some alteration of local conditions due to construction could be expected.

Museums mentioned in the text are the following: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; UCR, University of Costa Rica; FMNH, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.;

HSU, Humboldt State University, Arcata, California; LACM, Los Angeles County Museum of Natural History; USNM, National Museum of Natural History (Smithsonian Institution), Washington, D. C.; ANSP, Academy of Natural Sciences, Philadelphia; SDMNH, San Diego Museum of Natural History; TU, Tulane University. The following private collections are also cited: Sally Bennett Collection, Phoenix, Arizona; Helen DuShane Collection, Whittier, California; William Pitt Collection, Sacramento, California; Tom Rice Collection, Port Gamble, Washington; Donald Shasky Collection, Redlands, California; and Carol Skoglund Collection, Phoenix, Arizona.

BUCCINACEA

COLUMBELLIDAE

Mitrella Risso, 1826*Mitrella loisae* Pitt & Kohl, spec. nov.

(Figures 2a, 2b, 3a, 3b)

Diagnosis: A small, smooth *Mitrella* differing from other Panamic members of the genus in having a unique color pattern of irregular dots and wavy lines.

Description of Holotype: Shell small, slender, smooth, with 7 slightly convex whorls; ground color yellow; nuclear whorls 3, first 2 white, third yellow; first postnuclear whorl with faint brown wavy lines; second whorl with white band below suture, interrupted by wavy lines that merge into irregular dots; third whorl with narrow band of irregular brown dots below suture, followed by white

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band which is interrupted by wavy brown lines that merge into irregular dots; body whorl with narrow band of irregular dots below suture, followed by a white band which is interrupted by wavy brown lines which in turn merge into a series of irregular dots and wavy lines, all elongated in direction of growth; outer lip thickened, denticulate within; inner lip smooth except for 2 low folds; base of columella with about 10 spiral lirations. Height 5.3 mm, diameter 2.2 mm.

Type Locality: North side of Punta Coralillo, Bahía de Caldera, Puntarenas Province, Costa Rica (9°54' N; 84°44' W) (Figure 1), about 20 km S of the city of Puntarenas. There were 575 specimens collected by William and Lois Pitt on January 29-30, 1975.

Type Material: Holotype, CAS 60193. Paratypes (6) each to the following: CAS 60194-60199, AMNH, BMNH, UCR, FMNH, MCZ, HSU, LACM, USNM, ANSP, SDMNH, TU, DuShane Collection, Pitt Collection, and Skoglund Collection. The remaining specimens from the original lot are in the Pitt Collection. Variation among specimens in the original lot is from 4.4 to 5.2 mm in height. Some of the paratypes are juveniles as evidenced by the thin, non-denticulate outer lip.

Referred Material: 1) Playa Jaco, Puntarenas Province, Costa Rica (9°36' N, 84°38' W) (Bennett and Rice Collections, 1 specimen each, collected by Sally Bennett and Tom Rice on 25 April 1975); 2) El Rubio and Punta Mero, Tumbes Province, Peru (3°54' S, 80°53' W) (Shasky Collection, 21 specimens; SDMNH, 43 specimens; LACM, 39 specimens, collected by Donald Shasky, James H. McLean and Mario Peña on 16 April 1972); 3) south of Bocapan, Tumbes Province, Peru (3°44' S, 80°46' W) (SDMNH, 2 specimens; LACM 5 specimens, collected by Donald Shasky, James H. McLean, and Mario Peña on 12 April 1972); 4) Playas (reef at west end of beach), south side of Santa Elena Peninsula, Ecuador (2°38' S, 80°25' W) (Shasky Collection, 3 specimens; LACM, 2 specimens, collected by Donald Shasky and James H. McLean on 8 March 1970); 5) Cape San Francisco, Ecuador (approx. 0°37' N, 80°10' W) (LACM 1 specimen, collected on 23 February 1938, Hancock, bottom sample No. 586).

Discussion: *Mitrella loisae* is similar to *M. pulchrior* (C. B. Adams, 1852), but is more slender and differs in

color pattern in the following ways: *M. pulchrior* has rectangular white spots below the suture, separated by vertical dark blotches; whereas *M. loisae* has a white band below the suture, interrupted by wavy brown lines elongated in the direction of growth; *M. pulchrior* has clear-cut, fine dots on the body whorl; whereas dots on the body whorl of *M. loisae* are irregular in shape and in many cases merge into wavy lines. Other Panamic *Mitrella* treated in KEEN (1971) were not considered close enough to require comparison.

A southern form of *Mitrella loisae* from the above mentioned locations in Ecuador and Peru differs in having a paler ground color, and the wavy lines on the lower part of the body whorl tend to break into wavy dotted lines.

It is noteworthy that although extensive collecting has been done in Panama, there were no specimens of *Mitrella loisae* from that area in any of the major collections that we checked.

Mitrella pulchrior has been reported only from Panama (KEEN, 1971: 593). However, material that we have examined extends its range north to Matanchen, Nayarit, Mexico (CAS, collected by Faye Howard; LACM, collected by Gale Sphon), and south to Playas, Santa Elena Peninsula, Ecuador (Shasky Collection; LACM, collected by Donald Shasky, James H. McLean, and Mario Peña).

Etymology: The specific name honors the wife of the senior author who has given continual encouragement and been of much assistance in the field.

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Explanation of Figures 1 to 3

Figure 1: Aerial view of Punta Coralillo from 5000 m; arrow indicates the type locality of *Mitrella loisae*

Figure 2a: Ventral view of holotype of *Mitrella loisae*;

Figure 2b: Dorsal view of the holotype; height 5.3 mm

Figure 3a: *Mitrella loisae*, southern form, from El Rubio, and Punta Mero, Tumbes Prov., Peru; ventral view, height 5 mm (CAS)

Figure 3b: Dorsal view of the same specimen

Figure 1



Figure 2a



Figure 2b

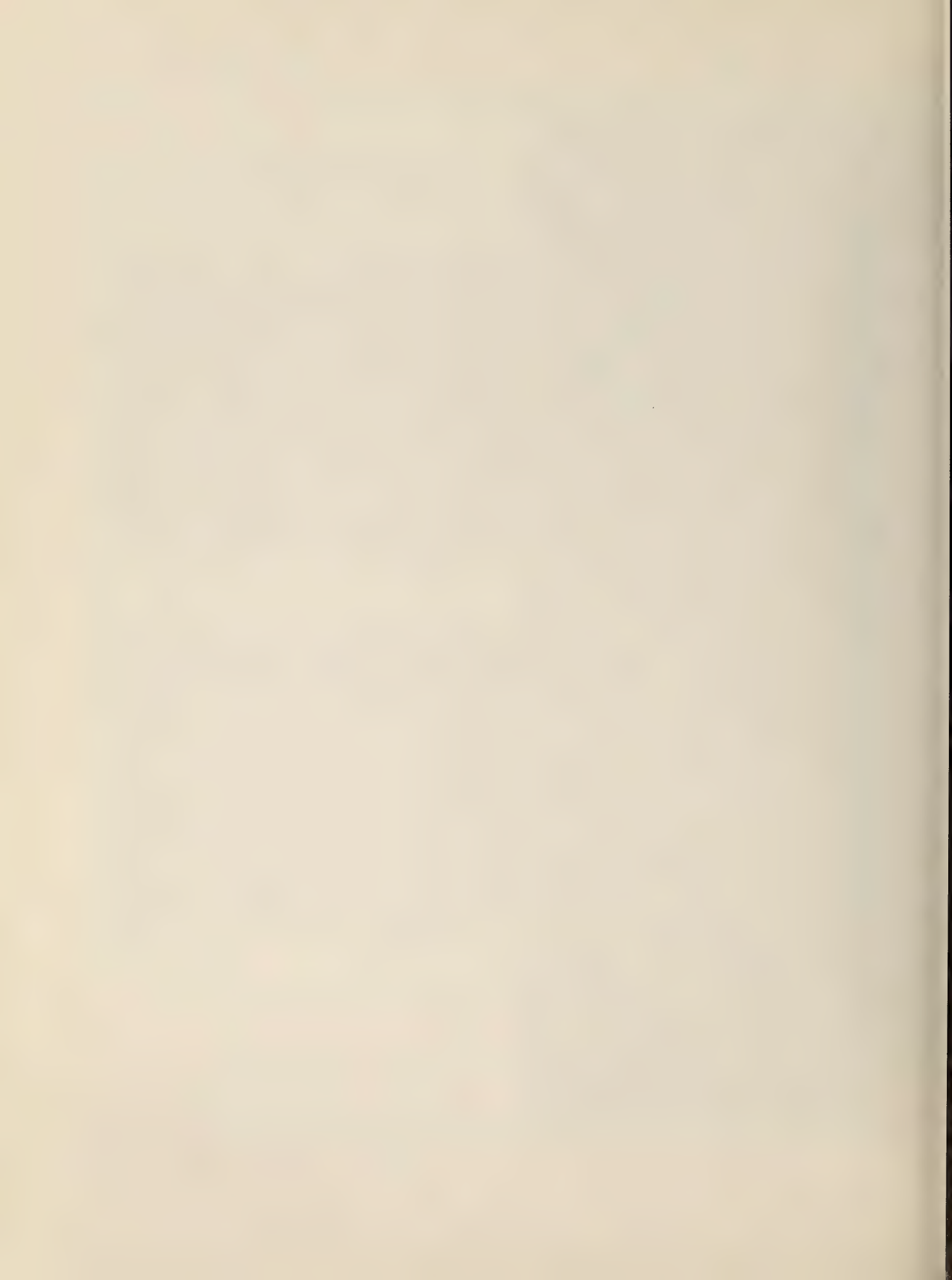


Figure 3a



Figure 3b





Evidence for an Additional *Littorina* Species and a Summary of the Reproductive Biology of *Littorina* from California

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(2 Text figures)

INTRODUCTION

STUDIES OF THE REPRODUCTIVE patterns of California littorinaceans revealed 2 morphologically distinct types of egg capsules produced by females identified as *Littorina scutulata* Gould, 1849. These egg capsules differed in their shape, dimensions, number of eggs per capsule and in the size and location of the hatching pore through which the veligers emerged. The developmental rate within the capsules was also found to differ between the 2 types. The occurrence of dimorphic penes among male *L. scutulata* further suggests that this taxon, as construed on the basis of shell morphology, is a composite of 2 morphologically similar species.

How significant are such differences in this group of snails? It has been shown by various authors, including WHIPPLE (1965), BORKOWSKI & BORKOWSKI (1969), ROSEWATER (1970) and BANDEL (1974), that egg capsule morphology is a discrete species character. BORKOWSKI & BORKOWSKI (*op. cit.*) further found that both shape and size of egg capsules were a "good species discriminator" for 3 *Littorina* species of a similar shell morphology that occur together on rocky intertidal shores in southeastern Florida. It is also evident from the studies of ROSEWATER (*op. cit.*) and BANDEL (*op. cit.*) that the utility of egg capsule morphology as a species character can be extended to faunal provinces rich in littorine species. Differences in embryonic and larval development can similarly be cited as species-specific traits. In males, the morphology of the penis has also been successfully employed in delineating littorinid species by ABBOTT (1954), WHIPPLE (*op. cit.*), ROSEWATER (*op. cit.*), as well as others.

Shells in littorinids, however, demonstrate greater variability than do egg capsules or soft parts. STRUHSACKER

(1968) has reviewed several examples of intraspecific variation within the Littorinidae. Her experimental work has further indicated that, for at least one species, variation in shell sculpture has a genetic basis, while survivorship of the 2 morphs depends upon the environment. Therefore, asynchronous environmental changes along a shoreline may serve to encourage variability among shells in a population. However, it is equally probable that a given environment may encourage convergence of shell characters of co-occurring species. The second hypothesis would serve to explain how 2 species might be considered as a single highly variable one, as present evidence suggests is the case for *Littorina scutulata*.

METHODS

Adult specimens of *Littorina scutulata* were collected from a variety of intertidal habitats from San Diego, California, U. S. A., north to Vancouver Island, British Columbia, Canada. Snails were packed damp in plastic bags, and hand-carried or air mailed in padded mailing bags. Specimens thus could be obtained throughout much of the species' range within 1 to 7 days without significant mortality. Upon arrival, snails were placed in Carolina Stacking Culture dishes (inside diameter 10.5 cm), half filled with filtered sea water at 15°C. The dishes of snails were then placed in a water bath of the same temperature and checked daily for egg capsules. Water was changed daily. Egg capsules were sorted on the basis of capsule shape and transferred to Stender dishes (inside diameter 5.3 cm) half filled with filtered sea water. Egg capsules were examined at 24-hour intervals until hatching. Following hatching, each egg capsule was examined and

point of hatching noted. The diameters of the hatching pore and of the capsule surface containing the pore were measured.

Individual spawning records, for fecundity estimates, were obtained by placing individual snails in the Stender dishes half filled with water and recording the presence or absence of egg capsules at 24-hour intervals. If spawning did not occur within 7 days, that snail was replaced; otherwise, snails were maintained until egg capsule production ceased. The number of eggs per capsule was recorded for all capsules produced in the laboratory.

This study was conducted at the Pacific Marine Station, Dillon Beach, California, from April until August 1973, and was continued at the Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island, during August 1974.

EGG CAPSULES AND FECUNDITY

The egg capsules produced by *Littorina* from California are planktonic. Within these capsules, the embryos develop to veligers before hatching. The number of eggs, and hence embryos, per capsule varies with species. In *L. planaxis* Philippi, 1847, no more than a single egg per capsule has been found in the several thousand examined. The number of eggs per capsule in *L. scutulata*, however, shows variability among capsules. This variation is stable for each capsule type, if either the range or mean of the number of eggs per capsule is considered. The differences in egg capsule morphology between the 2 *L. scutulata* morphotypes are described below.

Littorina scutulata, Type I: These egg capsules (Figure 1A) are slightly greater than 1 mm in maximum diameter. They consist of 2 biconcave discs separated by a central chamber containing the eggs. The overall appearance resembles that of an automobile wheel. The number of eggs contained in these capsules may range from 4 to 41 eggs, although 17 to 32 is usual. Variation in number of eggs per capsule is summarized in Table 1 for the stations studied.

The salmon-colored eggs prior to the first cleavage are 95.7 μ m in diameter. Each egg is enclosed within a transparent membrane 116.5 μ m in diameter. Fecundity estimates were not made for this group of *L. scutulata*.

Littorina scutulata Type II: The egg capsules described by BUCKLAND-NICKS *et al.* (1973), for *L. scutulata* are of this type. These capsules (Figure 1B) are shaped like inverted saucers and may contain 1 to 14 embryos, although 3 to 10 is usual (see Table 1). The egg capsule is slightly smaller than the Type I and contains fewer eggs. The eggs are salmon-colored, 105 μ m in diam-

Table 1

The range and mean of the number of eggs per capsule spawned by Type I and II *Littorina scutulata* during 1973.

Source	Approximate N. Latitude	Type I		Type II	
		range	mean	range	mean
Ucluelet, British Columbia	49°00'	—	—	1-4	2.9
Anacortes, Washington	48°30'	—	—	present	
Newport, Oregon	44°40'	4-35	17.3	—	—
Howard Creek, Mendocino Cty. California	39°45'	—	—	1-14	10.4
Sea Ranch, California	38°42'	14-35	25.3	7-9	7.9
Dillon Beach California	38°10'	5-34	22.6	—	—
San Luis Obispo, California	35°25'	present		3-13	7.3
Pismo Beach, California	35°10'	10-28	20.8	—	—
Gaviota, California	34°25'	6-41	23.8	3-6	4.4
S. Laguna Beach, California	33°32'	19-40	32.8	3-12	7.6
San Diego California	32°45'	7-32	18.0	2-11	4.2

eter and contained within an egg membrane 130.5 μ m in diameter.

Both Type I and Type II capsules are readily distinguished from the capsules of *Littorina planaxis* by size, number of eggs and capsule morphology; see Figure 1 and Table 3.

Fecundity estimates for isolated Type II *Littorina scutulata* from central and northern California indicate a lower egg production and longer period of spawning than reported by BUCKLAND-NICKS *et al.* (1973), for Puget Sound, Washington. They report that 3 females produced 896, 1034 and 1398 egg capsules within a 2-week period before capsule production ceased. These capsules contained from 3 to 4 eggs each so that total egg production per female was between 9900 and 13300. In the present study, 4 females from Mendocino County, California, isolated in 1973, produced 156 to 235 capsules with a combined egg production of 7220 eggs. Normalizing these data to a per-snail fecundity, the California snails were only half as fecund as the individuals from Puget Sound, although spawning lasted for 4 weeks with-

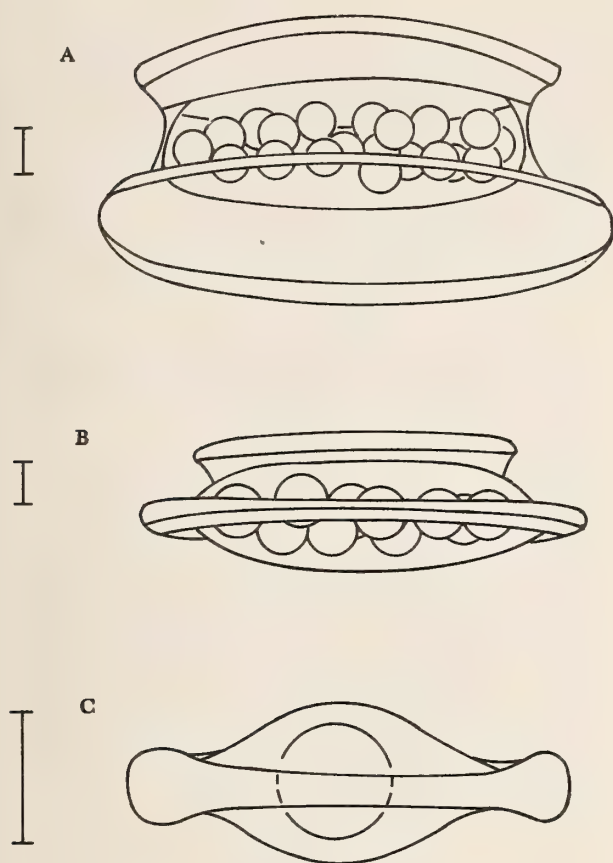


Figure 1

Pelagic egg capsules of California species of *Littorina*

- A) *Littorina scutulata* Type I, hatching pore, through which veligers emerge, forms on the lower capsule surface
 B) *Littorina scutulata* Type II, hatching pore forms on the upper capsule surface
 C) *Littorina planaxis*

Scale is 100 μ m

out reinseminating the females, 2 weeks longer than the Puget Sound snails. In 1974, 31 females were collected at the tip of Bodega Head, Bodega Bay, California, and isolated for fecundity estimates. The highest capsule production by a single snail was 872. These capsules contained 6024 eggs. A second snail produced 842 capsules containing 6807 eggs. The maximum length of a single spawning period for this group of snails was 2 weeks.

It appears, then, that California *Littorina scutulata* (Type II) produce fewer eggs and capsules while investing more eggs in each capsule than do Puget Sound snails.

With the data presently available, it is not possible to determine the source of differences in production. They may relate to population differences or to previous spawning history.

DEVELOPMENT AND HATCHING

In *Littorina scutulata*, Types I and II, the early development is synchronous (Table 2); the blastula forms in 24 hours, and the gastrula within 48 hours — 24 hours slower than in *L. planaxis*. The trochophore is reached in 4 days and from this point until hatching, development is asynchronous. In *L. scutulata*, Type I, the trochophore lasts for 24 hours before developing into a shelled veliger stage by day 5. In *L. scutulata*, Type II, the trochophore stage lasts 48 hours before developing into a shelled veliger on day 6. In both types, the veliger remains in the egg capsule for 2 days, emerging on day 7 in Type I and on day 8 in Type II. The developmental sequences of *L. planaxis* and the 2 *L. scutulata* are contrasted in Table 2.

Table 2

Summary of developmental events occurring within the egg capsule of California *Littorina* maintained at 15°C.

Day	<i>Littorina planaxis</i>	<i>Littorina scutulata</i> "Type I"	<i>Littorina scutulata</i> "Type II"
1	spawning	spawning	spawning
2	gastrula	blastula	blastula
3	trochophore	gastrula	gastrula
4	trochophore	trochophore	trochophore
5	veliger	veliger	trochophore
6	hatching	veliger	veliger
7		hatching	veliger
8			hatching

Hatching in *Littorina scutulata* s. l. is similar to that of *Lacuna pallidula* (da Costa, 1778) and *L. saxatilis* (= *L. rudis*) (Olivi, 1792) as reviewed by DAVIS (1968), in that the larvae emerge through a "hole." It is doubtful, however, that the "holes" are homologous to the hatching pores in *L. scutulata* s. l. *Lacuna pallidula* and *Littorina saxatilis* spend a proportionately longer developmental period in the egg mass, emerging as juveniles after rasping through their respective encasements with their radulae.

Littorina scutulata, in contrast, emerge as veligers at a predetermined site, the hatching pore. The pore is centrally located on one surface of the egg capsule and the larvae are incapable of emerging at any other point. This has been demonstrated by noting the fate of embryos in capsules with opposite disc surfaces lying against the bottom of the culture dish. In these capsules, the hatching pore, which is not visible prior to its completion, forms on the same surface, irrespective of orientation. Larvae in capsules whose hatching pore is adjacent to the bottom of the dish are unable to emerge although the pore is completely open.

The hatching pore in Type I *Littorina scutulata* is located on the capsule surface with the larger rim. It has a mean diameter of 250 μ m and represents an opening through which 2 larvae could simultaneously emerge. In Type II *L. scutulata*, the pore is located on the capsule surface with the smaller diameter and has a mean diameter of 340 μ m. This represents an opening through which 4 larvae could simultaneously emerge.

Rupture of the egg membrane is the first step in hatching and is apparently accomplished through a change in osmotic pressure. In both Type I and Type II *Littorina scutulata*, the egg membrane swells noticeably. BUCKLAND-NICKS *et al.* (1973) reported a $\frac{1}{3}$ increase in egg membrane diameter prior to hatching. The egg membrane can swell as much as 7 to 9 times the initial volume before hatching. The veligers emerge from their egg membranes before the hatching pore is evident, and may be actively involved in the formation of this opening. Movement within the capsule is limited but some swimming occurs. Abrasion of the inner capsule wall by the shell, employment of the snail's radula and release of lytic enzymes from the larvae or egg membrane fluid may contribute to the emergence process. It also seems probable

that the capsule wall is qualitatively different in the vicinity of the hatching pore or the point of emergence would be more variable. The presence of such a predetermined hatching pore is widely scattered through the mesogastropoda, having been previously reported in *Bithynia* (Hydrobiidae), *Lamellaria* (Lamellariidae) and *Trivia* (Eratoidae) by FRETTER & GRAHAM (1962); in *Strombus* (Strombidae) by D'ASARO (1965) and in *Monoplex*, *Mayena* and *Cabestana* (Cymatiidae) by LAXTON (1969). It is not previously known from Littorinaceans.

DISTRIBUTION OF CAPSULE TYPES AND PENIS MORPHOLOGY

The area of coastline over which spawning females were obtained is roughly equivalent to the central third of the range reported by OLDROYD (1927) for *Littorina scutulata*. The type of capsule produced did not correlate with wave exposure or the nature of the substrate (rock, sand, muddy sand). Furthermore, females producing the 2 morphotypic capsules were found to co-occur at 5 of the California stations. The ranges of these morphotypes differ, however. Type I capsules were found only as far north as Newport, Oregon, while Type II capsules were found over the entire study area. BUCKLAND-NICKS *et al.* (1973) did not record dimorphic capsules during their study at False Bay, Friday Harbor, Washington, nor were they present at the 2 stations reported here which bracket their study area. Based upon the absence of Type I capsules from Puget Sound to date, we may ascribe the capsule figured by BUCKLAND-NICKS *et al.* (*op. cit.*), here designated as Type II, to *L. scutulata sensu stricto* because the area studied by these authors is the type locality for this species (OLDROYD, *op. cit.*).

Table 3

Summary of the reproductive biology of *Littorina* from California.

	<i>Littorina scutulata</i> Type I	<i>Littorina scutulata</i> Type II	<i>Littorina planaxis</i>
Type of capsule	pelagic	pelagic	pelagic
Egg capsule diameter (mm)	1.1	0.7-1.0	0.3-0.4
Egg membrane diameter (μ)	116.5	130.5	100
Egg diameter (μ)	95.7	105	89
Number eggs per capsule	4-41	1-14	1
Number of days to hatching (15°C.)	7	8	6
Status at hatching	planktotrophic veliger	planktotrophic veliger	planktotrophic veliger
Shell width at hatching (μ)	169	155	137

A dimorphism in the penis of *Littorina scutulata* was also found (Figure 2). Considering only gross morphological detail, the form shown in Figure 2A has a conspicuous sperm groove running dorsally to a sub-terminal bulge. This form also possesses more hyaline granules than the second form and shows an area of canals with black pigmented borders where the penis inserts on the head. The penis in Figure 2B differs in the placement of the sperm groove, which runs laterally to the tip, and in possessing a large papilla on the dorso-lateral surface proximal to the curvature of the penis. No intermediate penis morphologies were observed.

The penes depicted in Figure 2A and B are both found in populations producing a mixture of the 2 egg capsule types. However, in a population from Anacortes, Washington (collected 13 May 1978 by Dr. A. J. Kohn) only the penis type shown in Figure 2A was found (15 males of 50 snails examined; sex ratio not significantly different from 2:1). The absence of dimorphic penes from Puget Sound *Littorina scutulata* therefore contributes additional evidence that populations in this area are monotypic. Following the reasoning used for assigning the identity of egg capsules, *L. scutulata* s. s. males are characterized by the penis morphology depicted in Figure 2A. The species heretofore considered to be *L. scutulata* is characterized by males possessing the penis type illustrated in Figure 2B and by females producing egg capsules like that shown in Figure 1A (Type I).

CONCLUSIONS

Based upon the differences in egg capsule morphology, developmental rates and penes between the 2 morphotypes of *Littorina scutulata*, it appears that *L. scutulata* is a complex of 2 species. Type II female snails are considered to belong to *L. scutulata sensu stricto* as are males with the penis morphology depicted in Figure 2A. The identity of *L. scutulata* Type I, however, is uncertain. GOULD (1849) described 2 additional species of *Littorina* from the Pacific Northwest, *L. plena* from San Francisco and *L. lepida* from Vancouver Island. A preliminary comparison of idiotypes of *L. plena* (MCZ 169298) and syntypes of *L. lepida* (MCZ 169222) indicates shell characters within the range of variation seen among female *L. scutulata* of both Types I and II. Therefore, *L. scutulata* Type I may be one of 2 species previously described by Gould or an as yet undescribed species which can co-occur with *L. scutulata* s. s. from at least Newport, Oregon south



Figure 2

Littorina scutulata penis types.

Scale is 1.0 mm

to San Diego, California. The co-occurrence, the tendency towards variable shell characters and the lack of additional material precludes a complete delineation of species characteristics at present. However, it is reasonable to expect that differences in radulae also exist and that radular differences can be correlated with egg capsules produced by a female or with penes in males. The difficulty with shell characters arises from the diversity of habitats these species occupy and the well known influence of habitat upon molluscan shell characters. It is

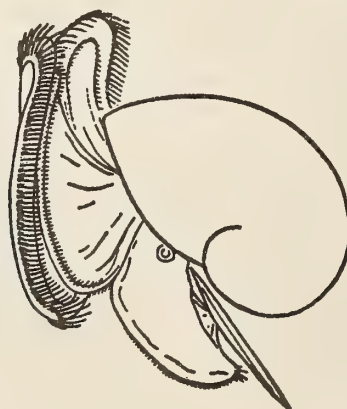
hoped that once *L. scutulata* is recognized as a complex of 2 species, differences in shell morphology and geometry independent of habitat can be identified. Gould used several parameters in his descriptions that can be quantified, including shell length, width, apical and basal angles, and aperture shape. It should be possible using multivariate statistics (*e. g.*, principal components, discriminant function analysis, etc.) to separate habitat variability from variation between the 2 species at present regarded as *Littorina scutulata*.

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The Epibiota of *Arca zebra* and *Arca imbricata*: A Community Analysis

BY

THOMAS B. SCANLAND

(4 Text figures)

INTRODUCTION

MARINE QUANTITATIVE, BENTHIC community analyses, as such, had their beginning with PETERSEN (1911 *et seq.*). A level-bottom community concept was developed by THORSON (1951 *et seq.*), who dealt principally with the infauna. The level-bottom community concept was expanded to include solid substrate habitats by NEWELL *et al.* (1959), who describe a rock-pavement habitat on the Bahama Bank.

Most marine, hard-bottom community analyses have been restricted to intertidal and nearshore environments (under strong influence of shoreline conditions). Of offshore community analyses, most have been qualitative in nature, and are generally lacking in the use of a consistent sampling unit. The use of a mollusk shell as a sample unit (as exemplified by WELLS, 1961, for an oyster community; and by WELLS *et al.*, 1964, for an offshore scallop community) provides a standard to which other standardized-unit community analyses can be readily compared, and renders the study more easily repeatable. This paper describes such a study in the northeastern Gulf of Mexico.

Literature on benthic communities in the Gulf of Mexico include TABB & MANNING (1961); DRAGOVICH & KELLY (1964); HEDGPETH (1953); PARKER (*e. g.*, 1960); PARKER & CURRAY (1968); PEQUEGNAT & PEQUEGNAT (1968) and WHITTEN *et al.* (1950). Two extensive series of offshore collections were made by the "Blake" and the "Oregon," the latter of which included several soft-bottom stations between Tampa and Cape San Blas. SUSIO (1973) has reviewed the literature on the eastern Gulf prior to the recent (1974-1978) Bureau of Land Management sponsored offshore environmental surveys.

While the availability of proper substrate limits the extent of offshore epifaunal communities, such substrate is offered in this study area by the limestone banks which LYNCH (1954) cites as one of the unusual features

of the Gulf. This bank is located 4.8 km S of Dog Island, Franklin County, Florida (29°46'N; 84°32'W), in 10 m of water. Similar limestone banks occur off Texas (PARKER, 1960) and the Bahamas (NEWELL *et al.*, 1959). Newell and his colleagues found the epifauna to be restricted by a covering of coarse, unstable sediments which are characteristic of these bank areas. The rock-pavement habitat provides attachment only for those organisms which can withstand the abrasion of, and avoid being buried by, these sediments.

In the area of Dog Island this niche is filled predominantly by 2 attached clams, *Arca imbricata* Bruguière, 1792 (= *A. umbonata* Lamarck, 1819) and *A. zebra* Swainson, 1833 (Pelecypoda; Arcidae). A greatly varied epifaunal community, as expected for this latitude, is found upon these arks. This paper is an analysis of that community.

METHODS AND MATERIALS

Approximately 140 arks, 30 to 100 mm in hinge length, were collected by hand for quantitative analysis, with the use of SCUBA in a relatively restricted part of the study area in June, September, and November, 1965. Another 110 arks for additional qualitative analyses were collected in 4 subsequent dives from December, 1965 to June, 1966. All were subjected to detailed examination under a dissecting microscope. First the valves were separated, and the soft-bodied species of epifauna (*e. g.*, polychaetes) were removed from each shell. These were counted, labelled and preserved for later confirmation of tentative identification. The shells were numbered and dried, and a numerical quantification and analysis of area occupied on each shell by each of several groups of organisms (*e. g.*, barnacles, ectoprocts, and serpulid polychaetes; see Table 2) was carried out for the initial 140 samples. All epifaunal species were identified to lowest possible taxon.

In addition, the distributions of encrusting algae as a

group, and of the encrusting sponge *Prosuberites microsclerus* were noted on an outline sketch for each ark shell. The shells were then measured for length (measured along the hinge), height (measured vertically from above the point of the umbo to the ventral margin of the shell), and thickness (measured as the greatest distance between right and left valves below the point of the umbo).

The sediment was analyzed by the method outlined by EMERY (1937). Water temperature, salinity, and visibility were also noted. All statistical tests used are outlined by WILCOXON & WILCOX (1964).

Frequency as used herein is the number of shells possessing a particular encrusting group divided by the total sample size (140). Density is the total number of individuals divided by the total sample size, and is given only for those groups which exist as solitary units (*i. e.*, are not colonial). The area occupied was obtained by estimating area covered by a particular encrusting group relative to the total area of the shell. These relative areas were then totaled and divided by the total sample size. The coverage of those species which rise above the surface of the ark was estimated by projecting their basal area onto the shell. The encrusting species which overlap, producing a stratified encrustation, were added separately. Consequently, in tabulations of the "area occupied" the total encrusted could exceed 100%, and the "area occupied" plus the "area unoccupied" commonly exceeded 100%.

RESULTS

PHYSICAL SETTING

The bottom salinity varied from 32.6 to 38.0‰. The temperature on the bottom ranged from 15.1°C in December to 24.0°C in June. Over 7 dives when these measurements were made the visibility on the bottom averaged 3 m and had a range of 1 to 7 m.

The sediment over the limestone is predominantly of sand-sized particles (as used by KRUMBEIN & PETTIJOHN, 1938). A breakdown of this sediment is given in Figure 1. The coarse fraction was principally of biological origin, the largest part mollusk shells and shell fragments. Other recognizable portions were contributed by corals, ectopods, crab and barnacle shells, and fragments from sand dollars and sea urchins.

The depth of the sediment varied from 0-15 cm over the limestone bottom. The bottom was, for the most part, flat with occasional elevations of 5-8 cm. On 2 dives (June, 1965 and June, 1966) clumps of *Ostrea equestris* were seen which formed heads up to ½ m in height. De-

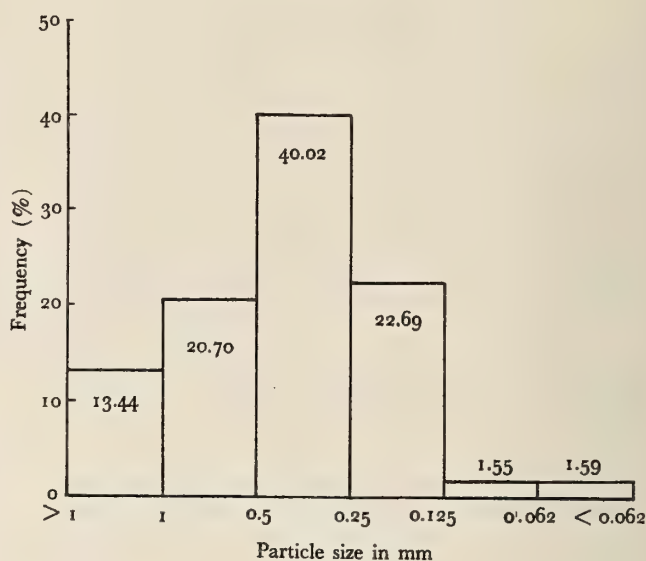


Figure 1

Histogram of Surface Sediment

pressions in the limestone not filled with sediment were rare, but were up to 15 cm deep.

BIOLOGICAL DESCRIPTION

In the macro-community the 2 most abundant fish species observed were a sea bass (*Centropristis* sp.) and the sand perch (*Diplectrum formosum*). Stomach analyses of specimens of both these fish obtained from the study area yielded organisms which were also found on the arks.

Since more than half of the observed area of the macro-community is shallow sediment, many organisms which are associated with coarse sand bottom occur here. Although these sand bottom species were not included in this study, the most prevalent macroinvertebrates were the sea stars *Astropecten* sp. and *Luidia* sp., and the polychaete *Chaetopterus variopedatus*. Some of the smaller, motile invertebrates included in Table 1 may also be from the sandy substrate. Another faunal segment of the macro-community not included in the present study are the epifaunal organisms which attach to the available solid substrate other than the arks. The most obvious species in this category were sponges including *Axinella* sp., *Tethya* sp., *Cinachyra* sp., and the gamma stage of *Cliona* sp.

Of the 140 arks selected for intensive analysis, 49 were *Arca imbricata* and 91 were *A. zebra*. Both of these ark

Table 1

Composition of the Epibiota from *Arca zebra* and *Arca imbricata*

Taxonomic Group	Remarks
Porifera	
<i>Axocella spinosa</i> (Wilson, 1902)	
<i>Cliona truitti</i> Old, 1941	
<i>Cliona</i> sp.	
<i>Cyamon vickersi</i> (Bowerbank, 1864)	
<i>Leucetta floridana</i> (Haeckel, 1872)	
<i>Prosuberites microsclerus</i> de Laubenfels, 1936, See Figure 3	
<i>Scypha barbadensis</i> (Schuffner, 1877)	
<i>Terpios fugax</i> Duchassaing & Michelotti	
<i>T. zeteki</i> (de Laubenfels, 1936)	
	15 other species including 1 lithistid
Coelenterata	
Anthozoa	
Zoantheria	
zooanthids	1 species
Actinaria	
<i>Aiptasimorpha texaenis</i> Calgren & Hedgpeth, 1952	1 specimen
	2 other specimens
Madreporaria	
<i>Cladocora arbuscula</i> (Le Sueur, 1820)	
	1 other species
Alcyonaria	
<i>Anthopodium rubens</i> Verrill, 1872	This low red alcyonarian found on 2 shells in the Nov. collection
Platyhelminthes	
Turbellaria	
Polycladida	1 species
Rhynchocoela	3 species
Aschelminthes	
Nematoda	Several species, these were found on most heavily encrusted shells, and particularly in detritus-filled barnacle tests and in the mud and mucous aggregations of errant polychaetes
Ectoprocta	
<i>Amathia</i> sp.	
<i>Antropora</i> sp.	
<i>Holoporella magnifica</i> Osburn, 1914	
	12 other species
Annelida	
Polychaeta	
<i>Ceratonereis tridentata</i> (Webster, 1879)	
<i>Cirriformia</i> sp.	
<i>Crucigera websteri</i> Benedict, 1887	
<i>Dodecaceria diceria</i> Hartman, 1951	
<i>Dorvillea rubra</i> (Grube, 1856)	This was the most frequently occurring species of errant polychaete; it was found most frequently in the tubes of serpulids and <i>Sabellaria</i> sp.
<i>Eumida sanguinea</i> (Oersted, 1843)	
<i>Eunice filamentosa</i> Grube, 1856	
<i>E. rubra</i> Grube, 1856	The mucous tubes of this species were on 8 of the 21 Nov. arks and extended over most of the surface of each of these shells This was the most frequently occurring serpulid
<i>Eupomatus sanctae crucis</i> Kroyer, 1863	
(See Hartman 1965, p. 574, 575)	
<i>E. gairacensis</i> Augener, 1934	
<i>Exogone dispar</i> (Webster, 1879)	
<i>Hydroides</i> cf. <i>crucigera</i>	
<i>H. microtis</i> March, 1863	

Table 1 (continued)

Taxonomic Group	Remarks
<i>H. norvegica</i> Gunnerus, 1786 <i>Hypsicornus torquatus</i> (Grube, 1877) <i>Lepidonotus</i> sp. <i>Loimia medusa</i> (Savigny, 1818) <i>Lumbrineris inflata</i> Moore, 1911	<p>This was the most frequently occurring sabellid</p> <p>This species occurred somewhat less frequently than <i>Dorvillea rubra</i> but was easily the second most abundant species; often occurred under ectoprocts, <i>Ostrea</i> sp., and <i>Chama</i> spp., and in the tests of barnacles</p>
<i>Lysidice ninetta</i> Audouin and Milne Edwards, 1833 <i>Megalomma lobiferum</i> (Ehlers, 1887) <i>Neanthes succinea</i> (Frey and Leuckart, 1847) <i>Nereis</i> sp. <i>Polycirrus</i> sp. <i>Polydora ligni</i> Webster, 1879 <i>P. websteri</i> Hartman, 1943 <i>Polydora</i> sp. <i>Pomatoceros caeruleus</i> (Schmarda, 1861) <i>Pomatostegus stellatus</i> (Abildgaard, 1789) <i>Sabella melanostigma</i> Schmarda, 1861 <i>Sabellaria floridensis</i> Hartman, 1944 <i>Sabellastarte</i> sp. <i>Scalabregma</i> sp. <i>Terebella rubra</i> (Verrill, 1873) (Homonym; Hartman, 1965: 527) <i>Terebellides stroemi</i> Sars, 1835 <i>Tharyx</i> sp. <i>Trypanosyllis vittigera</i> Ehlers, 1887 <i>Vermiliopsis bermudensis</i> (Bush, 1907) <i>V. cf. occidentalis</i> Spirorbids Flabelligerids	<p>2 species</p> <p>2 species</p> <p>18 other species</p> <p>5 species</p>
Sipunculida	
Mollusca	
Pelecypods	
<i>Anadara transversa</i> (Say, 1822) <i>Anomia simplex</i> Orbigny, 1845 <i>Arca imbricata</i> Bruguière, 1789	<p>1-30mm specimens of both these species were found in all three collections</p>
<i>A. zebra</i> (Swainson, 1833) <i>Chama congregata</i> Conrad, 1833 <i>C. macerophylla</i> Gmelin, 1791 <i>Chione grus</i> (Holmes, 1858)	<p>This was the more abundant of the two <i>Chama</i> species</p> <p>This species was the most abundant of the non-attached pelecypods</p>
<i>Ischadium recurvum</i> (Rafinesque, 1820) <i>Modiolus americanus</i> (Leach, 1815) <i>Musculus lateralis</i> (Say, 1822) <i>Ostrea equestris</i> Say, 1834 <i>Rocellaria hians</i> (Gmelin, 1791)	<p>A boring pelecypod, this species was found under a serpulid-ectoproct mass</p> <p>3 other species</p>
Gastropoda	
<i>Bulla occidentalis</i> A. Adams, 1850 <i>Calliostoma</i> sp. <i>Crepidula aculeata</i> (Gmelin, 1791) <i>C. fornicata</i> (Linné, 1767)	<p>This species was by far the more frequent of the two <i>Crepidula</i> species</p>

Table 1 (continued)

Taxonomic Group	Remarks
<i>Diodora listeri</i> Orbigny, 1853 <i>Mistrella lunata</i> (Say, 1826)	This snail and <i>O. seminuda</i> were the most abundant non-sedentary gastropods
<i>Murex florifer</i> Reeve, 1846 <i>M. fulvescens</i> Sowerby, 1834 <i>M. pomum</i> (Gmelin, 1791) <i>Odostomia dianthophila</i> Wells & Wells, 1961 <i>O. seminuda</i> (C. B. Adams, 1839) <i>Vermicularia knorri</i> Deshayes, 1843	
Arthropoda	This species occurred most frequently in the Nov. collection
Pycnogonida	
<i>Anoplodactylus lentus</i> (Wilson, 1878)	
Crustacea	
Ostracoda	2 species
Copepoda	3 species
Cirripedia	
<i>Balanus calidus</i> Pilsbry, 1916	These two species comprised the bulk of the sessile barnacles
<i>B. venustus niveus</i> (Darwin, 1854)	
<i>Kochlorine floridana</i> Wells and Tomlinson, 1966	
	2 other species
Malacostraca	
Isopoda	1 species
Amphipoda	
<i>Ampelisca agassizi</i> (Judd, 1896)	
<i>Elasmopus rapax</i> Costa, 1853	
<i>Lembos smithi</i> (Holmes, 1905)	
<i>Lysianopsis</i> cf. <i>alba</i>	
<i>Melita appendiculata</i> (Say, 1818)	This was the most frequently found amphipod
<i>Quadrivivio</i> cf. <i>lutzi</i>	
<i>Rildardanus laminosa</i> (Shoemaker, 1945)	
	This species was found inhabiting the empty tubes of a serpulid and of <i>Sabellaria floridensis</i> ; in the <i>Sabellaria</i> tube a male and a female were backed into the opposite open ends of the sand tube.
Decapoda	
<i>Mithrax forceps</i> (Milne Edwards, 1875)	
<i>M. pleuracanthus</i> Stimpson, 1871	
<i>Pagurus impressus</i> (Benedict, 1892)	
<i>Pilumnus sayi</i> Rathbun, 1897	The most abundant decapod
<i>Stenorynchus seticornis</i> (Herbst, 1788)	
	3 species of porcellanids
Echinodermata	
Echinoidea	
<i>Arbacia punctulata</i> (Lamarck, 1816)	
Ophiuroidea	1 species
Holothuroidea	1 species
Chordata	
Urochordata	
Ascidacea	3 species of solitary ascidians; 5 species of compound ascidians
Algae	
Chlorophyceae	
<i>Caulerpa</i> sp.	
Rhodophyceae	
<i>Botryocladia pyriformis</i> (Borgesen, 1920)	6 species of encrusting algae; 2 other species of Rhodophyceae

species attach to the substrate by means of a tough horny byssus which extends through the ventral gape of the paired valves. Thus an ark is aligned with its dorso-ventral axis perpendicular to the substrate and its broad hinge surface upward. Due to the greater thickness to length ratio of *A. imbricata* (Figure 2) the upper hinge surface

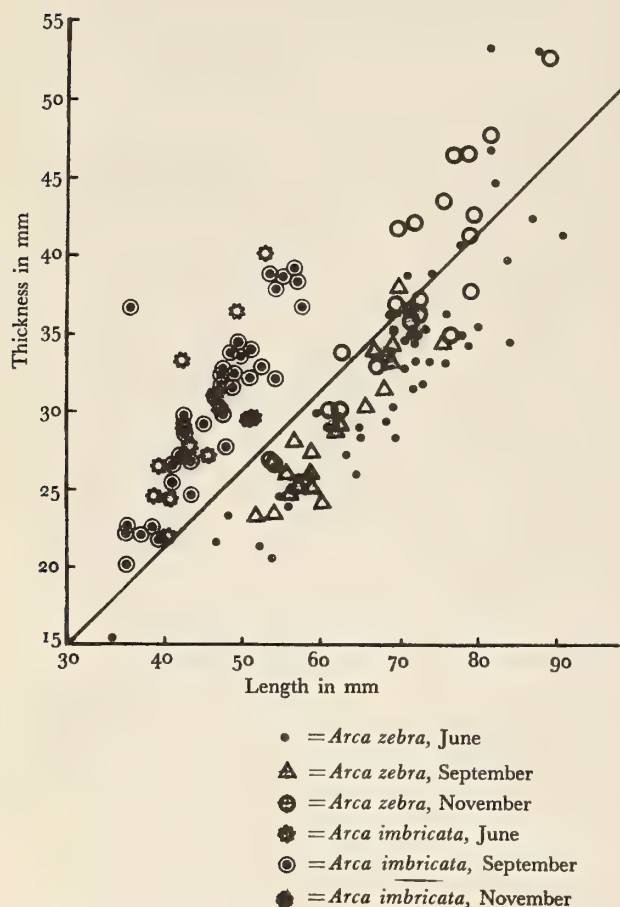


Figure 2

Length vs. Thickness for 140 Arks

in this species presents a larger surface area than in specimens of *A. zebra* of identical length. Because of this apparent difference in surface area available for attaching organisms, Wilcoxon's rank sum tests were carried out between the 2 ark species to determine if the data from the 2 could be combined. The tests were applied to 7 groups of frequently occurring encrusting organisms: acorn barnacles, boring barnacles, serpulids, *Chama* spp.,

Ostrea sp., encrusting algae, and encrusting ectopods. The data used for these tests came from the June and September collections which were tested separately (the November collection contained only 1 *A. imbricata*). Of the 14 tests, 12 showed no significant difference in the fouling of the 2 ark species at $\alpha = 0.05$. The significant differences found were for different encrusting groups and from different collections (*Ostrea* sp. in June; serpulids in September). Because of the lack of test significance in the fouling characteristics of the 2 ark species, neither is considered to exert a preferential influence on the epifauna involved. Therefore, the data from the 2 ark species have been considered together in this analysis.

In Table 1 is presented an annotated list of the 153 identified taxa found on the 2 arks. Protozoans were excluded from this analysis and most of the microcrustacea were lost in the collecting process. As an illustration, in June, 1966, one large *Arca zebra* was collected by encircling it with a jar before wrenching the shell from the substrate. From this specimen, more amphipods in both variety and abundance were collected than for the 140 arks which were quantitatively analyzed, combined.

Table 2 lists frequency, density and relative area occupied for 18 groups of encrusting organisms. The density is omitted for colonial species, and the area occupied is omitted for boring barnacles. All the figures are given for total sample size (June: 62; September: 57; and November: 21).

Evidence of seasonal change was shown to be significant at $\alpha = 0.05$ by the Wilcoxon rank sum test as follows for 4 groups of encrusting organisms: increase in area occupied by compound ascidians from September to November; by *Chama* spp. in both September and November over June; and by madreporarians in November over both September and June; and increase in frequency by *Sabellaria* sp. in September and November over June. Significant changes are indicated in Table 2.

Although most of the encrusting organisms were concentrated toward the middle of each valve, 2 consistent exceptions were noted. The encrusting sponge *Prosuberites microsclerus* was distributed in the posterior half of the shell, and predominantly along the upper posterior margin. In Figure 3, the locations of this sponge from 7 arks are superimposed on an outline sketch of an ark shell. The encrusting algae show a distributional pattern which is predominantly on or toward the dorsal surface. The extreme distributions of encrusting algae from 114 arks are shown in Figure 4.

Since the boring barnacle *Kochlorine floridana* was frequently found in encrusting algae, the possibility of a correlation between the area occupied by encrusting algae and the density of boring barnacles was tested by a modi-

Table 2

Frequency (as %), Density, and Area (as %) Summary
for 18 Groups of Sessile Organisms (N = 140)

		June	Sept.	Nov.
Sponges	f.	37.1	45.6	85.7
	area	2.0	3.0	2.4
Boring Sponges	f.	19.4	19.3	38.1
	area	4.2	3.8	11.2
Barnacles	f.	100.0	100.0	100.0
	d.	22.9	14.4	13.1
	area	5.3	3.1	4.2
Boring Barnacles	f.	64.5	75.6	90.5
	d.	18.2	13.5	52.8
Ectoprocts	f.	100.0	98.2	100.0
	area	12.7	6.1	8.9
Encrusting Algae	f.	72.6	91.2	95.2
	area	8.3	8.4	9.2
Upright Algae	f.	51.6	14.0	19.0
	area	0.3	0.3	0.1
Compound Ascidians	f.	9.7	1.8	52.4
	area	0.4	0.1	2.3
Solitary Ascidians	f.	4.8	1.8	0.0
	area	0.2	0.0	0.0
<i>Sabellaria</i> sp.	f.	72.6	98.2	100.0
	d.	1.9	9.9	9.8
	area	1.7	2.9	4.0
Madreporians	f.	38.7	54.4	95.2
	area	1.0	0.6	4.4
Zooanthids	f.	32.3	35.1	57.1
	d.	6.5	6.9	19.2
	area	0.6	0.7	1.2
<i>Chama</i> spp.	f.	98.4	94.7	100.0
	d.	7.5	5.8	12.6
	area	2.5	6.8	8.7
<i>Ostrea</i> sp.	f.	100.0	100.0	95.2
	d.	17.1	46.0	13.7
	area	3.2	6.6	1.7
<i>Arca</i> sp.	f.	45.2	38.6	95.2
	d.	0.8	0.9	3.3
	area	0.6	0.3	2.8
<i>Anomia</i> sp.	f.	17.7	10.5	14.3
	d.	1.5	0.1	0.1
	area	0.6	0.1	0.7
<i>Crepidula</i> spp.	f.	19.4	1.8	52.4
	d.	0.4	0.0	1.2
	area	0.3	0.0	0.9
Serpulids	f.	96.8	98.2	100.0
	d.	29.1	30.1	34.1
	area	7.4	2.9	3.9

nacles, ectoprocts, *Chama* spp., *Ostrea* sp., madreporians, serpulids, and the shell of the arks.

The possibility of a correlation between shell length (which is an indication of age) and boring sponge presence was also tested. A positive correlation at $\alpha = 0.05$ indicates that arks tend to acquire boring sponge with age.

Maximum density figures often varied considerably from the mean per sample for encrusting species. There

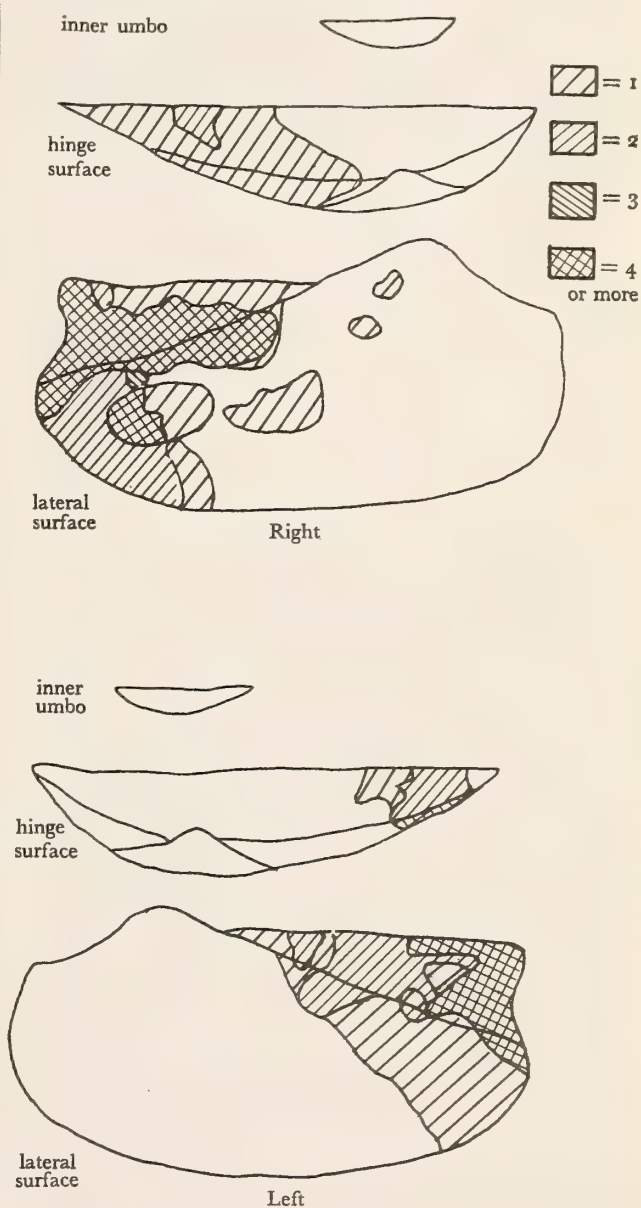


Figure 3

Distribution of the Sponge *Prosuberites microsclerus* on 7 Arks

fied Kendall rank correlation coefficient. The results of that test were not significant at the $\alpha = 0.05$ level. The *K. floridana* was also found bored into encrusting bar-

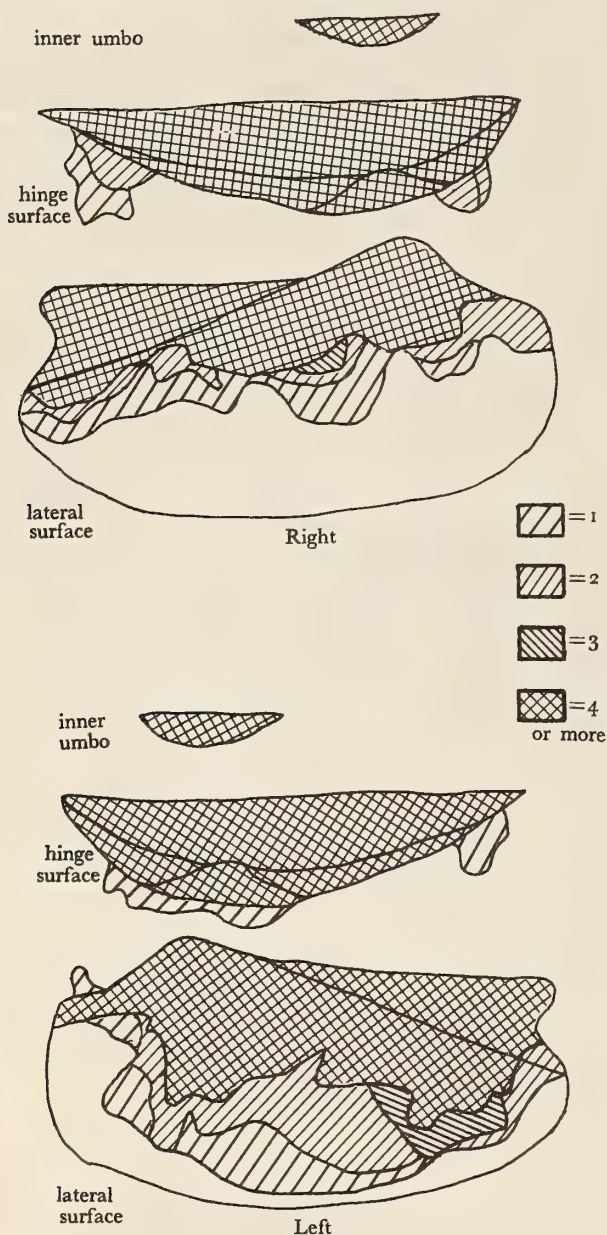


Figure 4

Distribution of Encrusting Algae on 114 Arks

were as many as 270 boring barnacles in a single ark and 7 other arks had densities greater than 100 per shell (overall mean 28.1). The sessile barnacles had maxima of 149 and 143 per ark ($\bar{x} = 16.8$).

Among mollusks, *Chama* spp. showed a maximum of 42, but only one other ark had more than 20 ($\bar{x} = 8.6$). Four arks had more than 100 *Ostrea* sp., with the maximum being 124 ($\bar{x} = 25.6$). Most of these oysters were spat. The maximum occurrence of *Arca* spp. on one another was 9, and the greatest density of *Anomia* sp. on any ark was 4. The *Crepidula* spp. had a similar low maximum density with 5 occurring on one ark.

Serpulids showed a density greater than 100 once with a maximum of 127. The next 2 high densities were 87 and 84 ($\bar{x} = 31.1$). *Sabellaria* sp. showed a high of 70 in September, and 7 more shells from the September and November collections had densities over 20. The maxima for the June collection were 11 and 7 (overall mean = 7.2).

DISCUSSION

A highly varied epifaunal community occurs on *Arca imbricata* and *A. zebra* in the described offshore habitat. During the period of observation the arks were the most abundant macroinvertebrates present and characterized this habitat. Their contribution to the community in the area observed as an unburied substrate for the epifauna exceeded that of any other species. For the macro-community there appear to be no other co-dominants.

Within the epifauna associated with these arks, the dominant members are sessile and sedentary filter and deposit feeders. These dominants are at or near 100% frequency, have relatively high densities, and occupy a relatively large area of the ark shells in all 3 collections analyzed. They are barnacles, ectopods, serpulids, *Chama* spp., and *Ostrea* sp. The area occupied by the oysters is less than that of the other 4, but its density is greater. The boring barnacles, because of their high density, and the encrusting algae, because of their high per cent of area occupied, are considered sub-dominants.

All of these organisms except the algae rely largely on plankton and detritus for nutrition. The upright algae are a minor part of the community, and this leaves only the encrusting algae as significant primary producers. Since they are not available to the filter feeders, the community is not self-sustaining, but must depend on productivity from outside the community to maintain it.

The most common errant members of the epifauna are 2 polychaetes, *Dorvillea rubra* and *Lumbrineris inflata*. Most of the polychaetes are filter or deposit feeders (including the cirratulids, flabelligerids, sabellariids, sabellids, serpulids, spionids, and terebellids). Other filter feeding members of this community not mentioned above include the remaining pelecypods and *Crepidula* spp., *Vermicularia* sp., ascidians and sponges.

With the exception of *Dorvillea rubra*, there are no frequently occurring carnivores resident upon the arks. Such carnivores as some of the fish, crustaceans, and gastropods, appear to move through the community, being only temporarily present near any given shell.

This distribution of producers and consumers leads to a trophic structure which, within the community, is highly imbalanced. Instead of the usual pyramid-shaped community trophic structure representation (ODUM & ODUM, 1959), a diagram of this community would be diamond shaped, with the central bulge representing the predominance of lower level consumers, and the narrow bottom and top representing the scarcity of available primary producers and the expectedly low number of resident higher level consumers.

The epifauna does not utilize the entire surface of the ark shell, but occupies the mid-portion of each valve. The anterior, posterior, and particularly the ventral margins generally have a thick periostracum which apparently discourages extensive encrustation. This thick periostracum is, however, used by errant polychaetes for shelter.

Approximately 50% of the shell surface is generally unused, a large part of this being on the dorsal surface. Although the encrusting algae are preferentially located in this position, few other organisms are. The general lack of organisms attached on this hinge surface can be largely attributed to the flexion of the valves. Rigid organisms which do occur on the dorsal surface cannot extend across the hinge. The vertical aggregations occurring on the umbo and the middle of the valves on many specimens also indicate that there is some disadvantage to settling on the margins of the valves. These vertical assemblages, up to 4 cm high, are both of one type of encrusting organism (particularly in barnacles, *Chama* spp., serpulids, or oysters) and composites of several types (particularly a barnacle-ectoproct-serpulid mass).

Though no arks of less than 30 mm in length were included in the quantitative study, many such small specimens were collected during the course of this study as epifauna on larger arks. The encrusting organisms which are first to settle on these small arks are mainly those which can attach to the periostracum, as only the dorsal surface of the umbo and the hinge area are bare. These early settling organisms are barnacles, ectoprocts, serpulids, *Chama* spp., *Ostrea* sp., and *Sabellaria* sp. As these fouling organisms grow, the periostracum is apparently weakened and pulled off the ark. Simultaneously the ark is producing new periostracum at the periphery resulting in a generally bare central and umbonal area on each valve which may then be further settled.

The only consistent further development with age (based on hinge length), not associated with season, is

the acquisition of boring sponge. This development is at least partly due to the removal of the periostracum as those larger arks which were sparsely settled and whose periostracum covered most of the shell were in no instance infested with boring sponge. There was also an indication that the acquisition of boring sponge was aided by infections by other borers, such as pelecypods, *Kochlorine floridana*, cirratulids, spionids and sipunculids.

Seasonal changes were significant for compound ascidians, madreporarians, *Sabellaria* sp., and *Chama* spp. The observed increase in frequency and density of *Sabellaria* sp. in September suggests that some of these tube worms had settled since June. The evidence of summer reproductive activity is corroborated by the observation of spawning by 4 *Sabellaria floridensis* from the June collection during the examination of ark shells in seawater.

Compound ascidians increased in frequency and area occupied in November. Although the total area occupied divided by the total sample size is relatively small (2.8%), this result is partially due to the low frequency. A few of the arks in the November collection were covered to the extent that nothing showed of the ark but an opening corresponding to the gape between the valves which was being fused over by the meeting edges of the ascidian. This assumed dominance in a few instances by compound ascidians has been previously observed (WELLS *et al.*, 1964).

The 2 groups of coelenterates studied quantitatively, the zooanthids and the corals, showed a similar winter increase. Though the apparent winter density for zooanthids of nearly 20 individuals per shell seems moderately high, the extreme high densities for the November collections were 118 and 121, and the average per shell possessing any zooanthids was nearly 34.

The phenomenon of dominance in a restricted part of each sample can be partly ascribed to the colonial nature of these forms. Where one individual or a small colony finds favorable conditions, quick development and expansion of the colony is possible. Relative increase of such forms in cold water may be due to their increased efficiency or the death or decreased efficiency of their warm season competitors, or both. In the case of compound ascidians, as in sponges, this patchy dominance is aided by a relative immunity to overgrowth by other organisms, allowing them, once settled, to avoid the problem of crowding and await favorable conditions for growth.

The distribution of encrusting algae along the dorsal surface and only rarely down the sides beyond the middle of the valve seems to be related to the availability of light. The distribution of the sponge *Prosuberites microsclerus* is more difficult to account for. Although there may be some benefit gained by currents produced at the

posterior end by the incurrent and excurrent canals of the ark, the shape of the ark shell is probably more important. There is a pronounced indentation extending from the umbo ventrally and posteriorly to the mid-posterior margin. The ribs are also strongly pronounced in this area in both species of ark. These 2 features may aid the sponge in becoming attached and remaining in the presence of strong abrasion. Most other portions of the shell are either covered by periostracum or are nearly smooth.

Evidence of growth in area occupied with a concurrent decrease in density is shown for *Chama* spp. These changes appear to be the result of rapid growth by the individuals which escape the mortality factors responsible for the decrease in population size. There was apparently settling by *Chama* spp. after September. This is not only evidenced by increased density in November, following the September density decrease, but also by the large number of less than 1 mm *Chama* individuals found in the winter collection. *Ostrea equestris* and both species of *Arca* also gave evidence in the form of small individuals (ca. 1 mm) that settling had occurred between September and November.

Of the communities to which this community in the northeastern Gulf of Mexico can be reasonably compared, 4 are sufficiently detailed to allow profitable comparisons. The rock-pavement habitat of the Bahama Bank described by NEWELL *et al.* (1959) bears comparison since it is a parallel habitat in a lower latitude. The most detailed of these 4 is the description of the calico scallop (*Aequipecten gibbus*) community by WELLS *et al.* (1964), which is a mollusk-centered, standardized-unit community analysis, and is, therefore, similar in treatment. It is a parallel community from a higher latitude, and is from a comparable habitat. Two others by PEQUEGNAT & PEQUEGNAT (1968) and by ALLEN (1953) make distance from shore and temperature inferences possible.

Newell *et al.* record only about 26 species of invertebrates, but they deal only with the more obvious forms (e.g., they list no polychaetes or crustaceans). The only pelecypod they mention is *Chama congregata* which also occurs in this community and which ranges from North Carolina to Florida and the West Indies. The *Arca* species are conspicuous by their absence, since the range of both species dealt with herein includes the Bahamas. The rock-pavement habitat in the Bahamas is dominated by gorgonaceans in the family Plexauridae which, Newell and his associates point out, are able to withstand the abrasion of the sand, as can the arks in the habitat off Dog Island. Neither the plexaurids nor any of the remaining species they list were observed in the study area and most are associated with tropical seas.

The species list provided by Wells *et al.* for the scallop epifauna includes 112 taxa. The scallop epifaunal community closely resembles that of the arks. Of the dominants they list, *Balanus venustus niveus*, *B. calidus*, *Pomatoceros caeruleus*, and *Sabellaria floridensis*, all are present in the community off Dog Island. *Pomatoceros caeruleus* occurs second in frequency to *Eupomatus floridanus* in the *Arca* epifauna; the *Sabellaria* approach dominance off Dog Island only in the winter. The collection of scallops in North Carolina was made in the first week of April. Both of the dominant barnacles in the scallop epifauna share a position of dominance on the arks as well.

It is pointed out by WELLS *et al.* (1964) that most of the species were of wide-spread distribution (35), or were distributed principally south of Beaufort, North Carolina (55), and that the community was tropical and subtropical in the majority of its affinities. At least 26 species are common to both communities, including *Arca zebra*. An important difference is in the lesser degree of success of *Ostrea equestris* and *Chama macerophylla* attained on the scallops, which were collected at the northern extent of the range of those 2 species. There are 153 taxa recorded from the *Arca* epifauna as compared with 112 from the scallops. The greater variety could be expected with the more southerly latitude of the Dog Island habitat. Other differences, such as the degree of importance of corals in these 3 communities, show the *Arca* rock-pavement community to be definably different from, though near its northern counterpart, the Carolinian epifaunal assemblage.

Spatial distribution differences between the epifauna of the arks and the scallops seem largely due to their different modes of existence. The arks are attached to the substrate and neither valve is preferentially selected by the sessile species of the epifauna. Imbalanced distributions which do occur on the arks vary from one individual to the next as to which valve has the heavier settlement, and these differences are due, at least in part, to varying proximity and orientation to neighboring individuals. The scallop (*Aequipecten gibbus*), on the other hand, had an average of 73% of its lower valve unfouled, while the upper valve had no free area. This disparity in fouling between valves is due to the scallop's resting on the same valve the majority of the time.

PEQUEGNAT & PEQUEGNAT (1968) report on a fouling study which was carried out concurrently with this research. Their work was carried out off Panama City, Florida, approximately 100 km west of Dog Island, with Cape San Blas about midway between the 2 study areas. They collected their data from floats placed at 5, 17, and 41 km offshore, from depths of 4 to 44 m, and to within 1 or 2 m

of the bottom. The floats were exposed for periods ranging from 2 weeks to 1 year.

Due to the differences inherent between an established bottom epifaunal assemblage and a variety of successional stages of a series of separate suspended assemblages, comparisons between the 2 species lists do not make the 2 appear very similar. A minimum of 15% of the species found on the arks are also found on the floats. However, a large number of the species listed from the floats are primary foulers, and very few of these species are present on the larger arks. For instance, 48 of the 187 taxa listed by Pequegnat & Pequegnat are hydroids, and none were found on the arks. Further, some of the species collected on the floats are associated only with that (*i. e.*, suspended or floating substrates) habitat, such as some of the hydroids and the 3 species of stalked barnacles they list. The similarities between the epifauna on the arks and the 3 Pequegnat stations decreased slightly with their increasing distance from shore; 18% (17 of 92), 16% (22 of 132), and 15% (18 of 114) species in common at the 5, 14, and 40 km stations, respectively.

Despite these differences, the same groups were important foulers in both investigations, namely the barnacles, ectoprocts, and serpulids. In the case of the barnacles, the 2 most important species, *Balanus calidus* and *B. venustus niveus*, were the same. The oyster *Ostrea equestris* was also an important member of both communities. Important genera from the *Arca* rock-pavement community missing from the floats include the arks, and *Chama* in the pelecypods, and *Sabellaria* in the polychaetes. The most abundant serpulid in the epifauna of the arks, *Eupomatus floridanus*, is a rare member of the fauna taken from the floats.

ALLEN (1953) found a greatly restricted epifauna (14 species) on *Chlamys septemradiata* in Scotland. His samples were from colder, deeper water, and on a finer substrate (mud) than in this study, all 3 of these factors tending to restrict the diversity of the epifauna (THORSON, 1957).

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Viability of Sperm in Two Land Snails, *Achatina fulica* Bowdich and *Macrochlamys indica* Godwin-Austen

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INTRODUCTION

ONE OF THE MOST IMPORTANT aspects of the reproduction and maintenance of a population level in terrestrial snails is the viability of sperms. The sperms received in copulation are stored temporarily in the storage organ of the snails. Information on the survival of sperms in the storage organ has been reported for only a few land snail species, viz.: *Helix aspersa* (TAYLOR, 1900) and *Limicolaria martensiana* (OWINY, 1974). Among aquatic snails, *Viviparus* (ANKEL, 1925), *Crepidula* (COE, 1942), *Lymnaea* (CAIN, 1956) and *Oncomelania* (ROTH, 1960, cited in HYMAN, 1967: 301) are on record. Nothing is known concerning this in *Macrochlamys indica*, but *Achatina fulica* kept in isolation has been reported to lay viable eggs up to 382 days (MEER MOHR, 1949). A series of experiments (RAUT, 1977) established that cross-fertilization is essential for laying eggs in both *A. fulica* and *M. indica*. A number of broods extending over a considerable period is obtained from a single specimen after one mating, though repeated mating is a common phenomenon.

MATERIALS AND METHODS

Twelve pairs of cage-reared snails each of *Achatina fulica* and *Macrochlamys indica* were selected immediately after their first mating since the attainment of sexual maturity. They were marked pairwise as A₁ A₂, B₁ B₂, . . . L₁ L₂, for *A. fulica* and a₁ a₂, b₁ b₂, . . . l₁ l₂ for *M. indica*.

Forty-eight cages, each measuring 50×50×50 cm, were used for the study. The sides and roofs of the cages were covered with 1.0 mm polythene net. All 48 cages were placed on soft, humus-rich soil in a shady place in the

Calcutta University campus, Ballygunge, Calcutta, exposed to natural light, temperature, humidity and rainfall. Only 1 mated snail was placed in each cage on March 30, 1975. The snails were kept active throughout the year by spraying with water when required, and a regular food supply was maintained until January 29, 1977, the date of termination of the experiments. The viable period of sperms was calculated from the date of the last brood since mating.

EXPERIMENTAL RESULTS

Of the 24 *Achatina fulica* B₁, D₁, F₁ and L₁ did not lay eggs. A₁, A₂, E₁, G₁, G₂, H₂ and L₂ laid their first brood on April 18, 1975, while the remaining 13 specimens laid eggs at different dates between the 26th and 61st day after mating. Most of the snails deposited 3 broods, while only 3 snails (A₂, G₂ and H₂) laid 5 broods. The last brood was laid by the snail K₂, 341 days after mating. The snails were maintained in a similar environment for a further period of 6 months. Subsequently they were dissected and the spermatheca as well as the talon were examined but no viable sperms were present. The viable period ranges (N=20) from 42 to 341 days with a mean, standard deviation and standard error of 149.2, 87.54 and 19.11 days, respectively.

Out of 24 *Macrochlamys indica*, e₁, g₁ and k₂ did not lay eggs. The first egg laying took place on April 8, 1975 by the snails b₁, b₂, c₂ and k₁, while others laid their first clutch between 12 and 39 days from the date of mating. The last clutch laid by the snails a₂ and l₂ was on July 19, 1976, i. e., 476 days after copulation. Most of the snails laid 6 broods during the period. They were maintained for another 6 months and dissection of spermatheca did not reveal viable sperms. The period of sperm viability ranges (N=21) from 63 to 476 days with a mean, standard deviation and standard error of 279.35, 101.54 and 22.71 days, respectively.

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DISCUSSION

In some pulmonates the spermatozoa are produced in the ovotestis throughout the year and the ovotestis duct remains packed with sperms. Fertilization is dependent on the oogenesis cycle (CHATTERJEE, 1970; FRETTER & PEAKE, 1975; RAUT, 1977).

Wide variations in the viable periods of sperms both in aquatic and land snails have been reported by a number of workers. In general, the period is longer in land forms. In aquatic snails the sperms are active for at least 116 days in *Lymnaea* (CAIN, 1956), 150 days in *Viviparus* (ANKEL, 1925), 365 days or more in *Crepidula* (COE, 1942) and 540 days in *Oncomelania* (ROTH, 1960, cited in HYMAN, 1967: 301). In land snails, the period is 520 days in *Limicolaria* (OWINY, 1974) and 1460 days in *Helix* (TAYLOR, 1900). MEER MOHR (1949) observed that *Achatina fulica* laid viable eggs as long as 382 days. It appears that the sperms were viable for about 366 to 367 days, since *A. fulica* required 16 to 17 days for the development of fertilized eggs. The gestation period and the time required for fertilization were observed to be 20 and 3 to 4 days, respectively (RAUT, 1977).

From the limited information available on the viable period of sperms in prosobranchs, basommatophorans and pulmonates it appears that the period varies with species and within the species. The interspecific variation in sperm viability is probably a specific character, which is supported by the fact that in spite of living in the similar environment, the period differs considerably in *Achatina* and *Macrochlamys*. Intraspecifically such variation is presumably influenced by the habitat, since the viable period of sperms in *A. fulica* was at least 366 - 367 days in Sumatra (MEER MOHR, 1949) and 42 - 341 (average 149.2) days in Calcutta.

The long viable period of sperms in pestiferous snails and their ability to lay a number of broods after one mating make it possible for them to populate a new area with the introduction of a single gravid specimen, and this demands our constant vigilance to prevent further spread of agri-horticultural snail pests.

SUMMARY

1. The maximum viable periods of sperms observed in *Achatina fulica* and *Macrochlamys indica* were 341

and 476 days, respectively. It ranges from 42 to 341 (149.2 ± 87.54) days in *A. fulica* and 63 to 476 (279.35 ± 101.54) days in *M. indica*.

2. The interspecific variation in sperm viability is probably a specific character, whereas intraspecific variation is presumably governed by the bio-physical factors of the habitat.
3. The long viable period of sperms is an additional advantage to the species in permitting it rapidly to populate a new area.

ACKNOWLEDGMENT

The authors wish to express their sincere thanks to the Indian Council of Agricultural Research for financial support.

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1956. Studies on cross-fertilization and self-fertilization in *Lymnaea stagnalis oppressa* Say. Biol. Bull. 111: 45 - 52
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1977. Ecology and ethology of *Achatina (Lissachatina) fulica fulica* Bowdich and *Macrochlamys indica* Godwin-Austen. Ph. D. Thesis, Calcutta Univ., Calcutta
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1900. Monograph of the land and fresh water Mollusca of the British Isles. 1. Structural and General. Leeds, Taylor Bros. 454 pp.

NOTES & NEWS

Literature Cited

Recognition

of *Cyclocardia ovata* (Riabinina, 1952)

in the Eastern Pacific

BY

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THANKS TO THE COURTESY of Dr. Alexander I. Kafanov of the Institute of Marine Biology in Vladivostok, a better understanding of certain eastern Pacific members of the genus *Cyclocardia* is now possible. Dr. Kafanov has sent a number of specimens of living and fossil species of this genus from the northwestern Pacific and Siberia not previously represented in collections in this country, as well as a copy of RIABININA (1952), evidently not previously available in U.S.A. libraries. All of this material has been placed in the California Academy of Sciences.

One significant discovery permitted by this material was that the eastern Pacific specimens I tentatively referred to "*Cyclocardia* cf. *rjabiniinae* (Scarlato, 1955)" (COAN, 1977: 379-380; fig. 10) is instead probably *C. ovata* (Riabinina, 1952). The California Academy of Sciences Type Collection now contains paratypes of *C. rjabiniinae* (CAS 60014). Shells of *C. ovata* differ from those of *C. rjabiniinae* in having higher, more central beaks and in having a more arched hinge with proportionately smaller teeth. *Cyclocardia ovata* was originally proposed as *Venericardia* (*Cyclocardia*) *borealis* "var." *ovata* Riabinina, 1952. This is not a homonym of *Cardita ovata* C. B. Adams, 1845, which, according to DALL (1903: 706), is a venerid.

The distribution of *Cyclocardia ovata* (Riabinina, 1952) is now known to include the north and south coasts of Chukotsk Peninsula, and south in the western Pacific to Sakhalin Island. In the eastern Pacific, the species occurs near the Pribilof Islands and from Amchitka Island eastward to Kodiak Island.

ADAMS, CHARLES BAKER

1845. Specierum novarum conchyliorum, in Jamaica repertorium, synopsis, ... Boston Soc. Nat. Hist., Proc. 2: 1-17 (Jan. 1845)

COAN, EUGENE VICTOR

1977. Preliminary review of the northwest American Carditidae.

The Veliger 19 (4): 375-386; 4 pls. (1 April 1977)

DALL, WILLIAM HEALEY

1903. Synopsis of the Carditacea and of the American species.

Proc. Acad. Nat. Sci. Philadelphia 54 (4): 696-719 (20 Jan. 1903)

RIABININA, N. V.

1952. Carditacea Chukotskogo Moria i Beringova Proliva. [Carditacea of the Chukotsk Sea and Bering Strait.] Akad. Nauk, SSSR, M., Krainii Severo-Vostok SSSR 2 Izd.-vo: 279-285; 2 figs.

SCARLATO, OREST A.

1955. Phylum Mollusca: Class Bivalvia. In: E. N. Pavlovskii (ed.), "Atlas of the invertebrates of the far eastern seas of the U. S. S. R." Akad. Nauk Moscow, 243 pp.; 66 pls. [translated by the Smithsonian Institution, 1966; 464 pp.]

On the Relevance

of Small Gastropod Shells

to Competing Hermit Crab Species

BY

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STUDIES ON GASTROPOD SHELL utilization by adult hermit crabs have demonstrated that the choice of a shell can influence crab survivorship (REESE, 1962; VANCE, 1972b) and fecundity (BOLLAY, 1964). The literature on hermit crab competition in shell-limited environments has focused attention on shell utilization patterns of adult crabs (BOLLAY, *op. cit.*; HAZLETT, 1970; KELLOGG, 1971; CHILDRESS, 1972; VANCE, 1972a, 1972b; GRANT & ULMER, 1974; WANG, 1975; BACH *et al.*, 1976; FOTHERINGHAM, 1976). While the optimal-sized shell may contribute to enhanced adult fecundity and survivorship, an additional factor

may play a crucial role in the outcome of competition among hermit crab species: competition among juveniles for small shells.

Consider 2 species of hermit crabs competing in a shell-limited environment, where there are fewer small, empty snail shells than newly-metamorphosed crabs. Interspecific competition among juvenile hermit crabs for their first shell is expected to be intense. The most abundant species of juvenile crab will not necessarily be the most successful. Aggression, size, and ability to locate uninhabited shells could influence the relative success of each species. The availability of small shells acts to regulate the total number of juveniles of each species recruited into the adult populations. This model allows several predictions:

1. Competing hermit crab species should evolve mechanisms reducing the intense juvenile interspecific competition for small shells. Temporal resource partitioning is one such mechanism. Species breeding during different periods of the year could insure that all available small shells are occupied by juveniles of that species. REESE (1968) and SAMUELSON (1970) reported different periods of peak reproductive activity for hermit crabs in Hawaii and Norway, respectively. REESE (*op. cit.*) reasoned that competition for food among planktonic larvae was responsible for the observed periodicity, but competition for small shells is an equally viable hypothesis.
2. The period of larval development for a competing hermit crab species may be reduced as compared to a species which does not compete for shells. This would be a form of exploitative competition in which larvae settling first obtain shells.
3. If tiny shells do not persist in the environment for a significant period of time, hermit crab species should be expected to regulate their reproductive activity to coincide with maximum shell availability.
4. Selection for large larval size or greater aggressiveness could enhance juvenile survivorship. Larger larval size would allow a species to select larger shells immediately and avoid competition if the 2 species settle at the same time. A more aggressive animal may have greater success in shell fights.

Competition among adult females for an optimum-sized shell may be relatively unimportant. We suggest

that hermit crab competitive ability is not principally correlated with clutch size. The reduced clutch size of a female would not necessarily affect the probability of her offspring obtaining their first shell. The ability of juveniles to secure a shell may be the major determinant of the outcome of competition among hermit crab species in shell-limited environments.

ACKNOWLEDGMENTS

We are grateful to A. Davis and E. H. Jillson for discussions of these ideas, and to J. S. Cobb and W. R. Ellington for comments on the manuscript.

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1970. The biology of six species of Anomura (Crustacea, Decapoda) from Raunefjorden, Western Norway. *Sarsia* 43: 25-52
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1972a. Competition and mechanisms of coexistence in three sympatric species of intertidal hermit crabs. *Ecology* 53: 1062-1074
1972b. The role of shell adequacy in behavioral interactions involving hermit crabs. *Ecology* 53: 1075-1083
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1975. Agonistic and shell fighting behaviors among two sympatric species of hermit crabs (Anomura: Paguridae). M. S. thesis, Univ. Delaware, 100 pp.

Soviet Contributions to Malacology in 1977

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INTRODUCTION

ONCE AGAIN WE OFFER a translation and commentary on the recent Soviet literature in malacology which was mostly published in the year 1977 and abstracted in the Referativnyy Zhurnal. This annual contribution to the community of interested readers (see *The Veliger* 20 (4): 390-398; 19 (4): 440, for last year's listing and for references to earlier resums, respectively) will hopefully continue to be useful. With few exceptions, we have followed the editors of the Referativnyy Zhurnal in their arrangement of categories.

Since specialists can proceed directly to items of particular interest in special taxonomic categories, we have constricted these introductory remarks to more general topics and to the citations of more or less important papers in which new taxa, new revisions or little known areas are covered.

The diversity of problems to which Soviet workers addressed themselves in 1977 (and 1976 for a few items) is as great as ever, though there is a noticeable reduction in topics related to commercial utilization of molluscan species and their otherwise applied usefulness. Also, for example, few papers deal with mollusks as vectors in parasitic diseases.

Of greatest importance to non-Soviet students are several works which propose more or less far reaching changes in the higher ranks of molluscan taxonomy and systematics. Such are papers by Shileiko on Docoglossa, Chistikov on Scaphopoda, Starobogatov on marine pulmonates, Scarlato and Starobogatov on Polyplacophora—a complete revision with 1 new order and 2 new suborders—and Shileiko on the Pulmonata. The last is a very important paper which has been expanded elsewhere and which casts doubt on the prevailing urethra-centered classification of the Stylommatophora.

Novelties of lower rank were not neglected. Such were introduced by Sirenko (*Lepidopleurus*), Izzatullaev (*Val-*

vata), Minichev (*Cylichna*—plus a new subgenus *Cyclinoides*), Minichev (*Pneumodermopsis*), Lus (northern buccinids), and Moskalev (Cocculinidae with 6 new monotypic genera).

Zoogeographical data from previously unknown or little known regions are also provided: Pirogov (Volga Delta), Gundrizer and Ivanova (Tuva), Boev (Bashkiria), Starobogatov and Budnimova (Chukotsk Peninsula), Guseva (Irkutsk), Iogansen, Mukhitdinov (south central Siberia), Izzatullaev, Mukhitdinov (Tadjikistan), Dolgin *et al.* (subarctic Siberia), Likharev, Damyanov *et al.* (Bulgaria), Guntya (Dniester), Akramovski (Armenia), Rodionov *et al.* (Seliger Lake), Cheremnov (Khabasia), and Reznik (Kuma River).

Problems in molluscan evolution are treated by Barskov, Shimansky, Nesis (cephalopods), and Neifakh (*Lymnaea stagnalis*). Data on the evolution of the molluscan nervous system are provided by Minichev, and Starobogatov discusses the evolution of cephalopod tentacular apparatus.

Interesting biological data on *Turtonia minuta* and *Hiattella arctica* are discussed by Matveeva and Maksimovich, on the genus *Spinula* (Malletiidae) by Filatova, and on the hydrobiid *Semisalsa dalmatica* by Chukchin.

The following list explains abbreviations and acronyms used in this résumé:

- AN – Akademiya nauk (Academy of Science)
- Biol. Morya – Biologiya Morya (Marine Biology)
- DVBPI – Trudy Biologo-Pochvennyi In-ta. Dal'nevostochnyi Nauchnyi Tsentr, AN SSSR (Proceedings of the Soil Institute of the Far Eastern Scientific Center of the AN USSR), Vladivostok
- Dokl. Akad. Nauk SSSR (Reports from the Academy of Science of the USSR)
- EEMB – Eksperim. Ekologiya mor. bezpozvonochnikh (Experimental study, ecology and morphology of invertebrates), Vladivostok
- ES – English summary
- IFML – Issled. fauny morei, Leningrad, Nauka (Studies of marine fauna, Leningrad Science Press)
- MN – Mollyuski, ikh sistema, evolutsiya i rol' v prirode. Nauka. (Mollusks, their systematics, evolution and significance in nature. Science Press), Leningrad
- SPZM – Sovrem. probl. zool. i soversh. metodiki yeye prepodavaniya v vuse i shkole, perm' (Contemporary problems of zoology and the improvement of teaching in institutions and schools)
- TRO – Trudy Instituta Okeanologii. Akademiya Nauk SSSR. (Transactions of the Institute of Oceanology, Academy of Science, USSR)
- VINITI – Vsesoyuznyi Institut Nauchnoi i Tekhnicheskoi Informatsii (All Union Institute of Scientific and Technical Information), AN, SSSR
- VPS – Vopr. paleontol. i stratigr. (Problems of paleontology and stratigraphy), Azerbaidzhan

ZOB - Zhur. Obshch. Biol. (Journal of General Biology)
 ZZ - Zoologicheskii Zhurnal (Zoological Journal)

We thank Mrs. Mary Jo Dent for her careful typing of the manuscript.

GENERAL

AKRAMOVSKY, N. N.

1976. The molluscan fauna of the Armenian Socialist Soviet Republic. Erevan, AN ArmSSSR, 287 pp.; illust.

[In this popular text, 155 species are listed and described]

ALI-ZADE, Ak. A. & S. A. ALIEV

1976. On the problem of the biogeochemistry of Pontian mollusks. VPS, Vyp. I, pp. 50 - 56

[40 species of 12 genera were studied for contents of calcium, magnesium, manganese, iron, aluminum, silicon, titanium, copper, strontium, barium and nickel. Even insignificant environment changes promote the formation of various structural peculiarities in the shell]

BOEF, V. G.

1975. On the freshwater molluscan fauna of Bashkiria. Uch. zapiski (educational notes), Bashkir Univ. Vyp. 76: 25 - 32

[25 gastropod species and 12 bivalve species, of which 5 were cited for the first time, were found in 7 regions of Bashkiria. 32 species were found in the Volga Basin and 28 in the Ural River Basin]

CHEREMNOV, A. D.

1976. On the ecology of the freshwater mollusks of Khakasia. SPZM, pp. 33 - 34

[A list of the freshwater bivalves and gastropods of the left bank of the Yenisei River is accompanied by ecological notes]

DOLGIN, V. N., B. G. IOGANZEN, E. A. NOVIKOV & YA. I. STAROBOGATOV

1976. The freshwater mollusks of subarctic Siberia. Biol. osnovy ryb. kh-va resp. Srednei Azii i Kazakhstana (Basic biology of the fishing industry in the republics of Central Asia and Kazakhstan), Dushanbe, pp. 69 - 71

GONTYA, F. A.

1975. Some results of the studies of mollusks from the Dniester Basin. MN, Sb. 5, pp. 60 - 62

[78 species of bivalves and gastropods in 36 genera and 15 families are noted]

GUNDRIZER, A. N., M. A. IVANOVNA & E. A. NOVIKOV

1977. The freshwater mollusks of Tuva. Trudy NII biol. i biofiz. pri Tomsk Univ. 8: 60 - 63

[59 species and subspecies (6 prosobranchs, 21 pulmonates and the remaining bivalves) constitute this fauna which bears a mixed Palearctic appearance. 26 Palearctic, 20 East Siberian, 10 European-Siberian and 3 Siberian taxa characterized the Yenisei Basin in Tuva. Also some Holarctic, western Mongolian and Sino-Indian species are present. The fauna of Ubsanura and Kobdo was less intensely studied]

IL'INA, L. B., L. A. NEVESSKAYA & N. P. PARAMONOVA

1975. Regulation of molluscan evolution in isolated and partially isolated bodies of water in the Late Miocene and Early Pliocene of Eurasia. MN, Sb. 5, pp. 188 - 190

[Certain trends are noteworthy in such bodies of water: 1) a very small number of families is present in comparison to the relatively large number of families and genera which constitute the source fauna in nearby, open marine basins; 2) a great increase in the number of species and their populations, especially endemics; 3) the predominance of representatives of euryhaline marine families; 4) the presence of brackish water forms; 5) the subdivisions of trophic regimes and the narrowing of niches. (The subject expressedly relates to the radiation of cardiids in the Ponto-Caspian Basin during the late Tertiary)]

IOGANZEN, B. G. & V. N. DOLGIN

1976. The freshwater mollusks of northwestern Siberia and their qualitative development. Vopr. biol. i agronomii (Problems in biology and agronomy), Tomsk, pp. 67 - 77

[65 gastropod and bivalve mollusks are known from the various reservoirs in this distinct biota]

IOGANZEN, B. G., E. A. NOVIKOV & A. D. CHEREMNOV

1976. Freshwater mollusks of south central Siberia. Probl. ekologii, Tomsk, 4: 125 - 136 (ES)

[In this survey, 38 species of gastropods and 43 species of bivalves were treated]

IZATULLAEV, Z. B.

1976. On the freshwater molluscan fauna of northern Tadzhikistan. Biol. osnovy ryb. kh-va resp. Srednei Azii i Kazakhstana (Basic biology of the fishing industry in the republics of Central Asia and Kazakhstan), Dushanbe, pp. 83 - 84

IZZATULLAEV, Z.

1977. New and little known freshwater mollusks of Central Asia. ZZ 56 (6): 948 - 950 (ES)

[*Valvata (Cincinna) gafurovi* is described as new from mountain lakes (Sulukty-Sai) in the East Pamirs of the Gorno-Badakhshanskaya Autonomous Republic, Tadzhikistan. Also *Sphaerium corneum* and *Musculium creplini* were found in the East Pamirs]

KOKOCHASHVILI, G. V.

1976. Materials for a dictionary of Russian-Georgian conchological terms. Tbilisi, 80 pp.

MINICHEV, Yu. S.

1975. The origin of the molluscan nervous apparatus. MN, Sb. 5, pp. 15 - 18

POZDNYAKOVA, L. A.

1976. On the possibility of complex estimates of the determination of calcium and magnesium contents in molluscan shells in connection with paleo-temperature analysis. EEMB, pp. 140 - 142

SADYKHOVA, I. A.

1976. Shell marking in the study of mollusks. EEMB, pp. 154 - 155

[A survey of modern methods with a list of mainly English language papers]

VOLOSHINA, M. I.

1977. Terrestrial mollusks from the upper quarter of the Central Priputya [Formation] of the basin of the Chugur River. Faunal and floral complexes in the cenozoic of the Pre-Black Sea. Kishinev, Shtiintsa, pp. 57 - 61

[This is the first account of the land and freshwater mollusks of the late Anthropogenetic of the region. An attempt is made to clarify the topographic-climatic conditions of ancient Moldavia]

YAROSLAVTSEVA, L. M.

1976. A study of the adaptation to the freshening of water in several species of littoral and estuarine marine mollusks. EEMB pp. 189 - 190

ZOLOTOREV, V. N.

1976. Perspectives in the study of the growth rates and ages of mollusks. EEMB, pp. 81 - 84

[The oldest specimen of the Far Eastern mussel, *Crenomytilus grayanus*, was calculated to be 104 years. Other species of bivalves were listed from 22 to 61 years. Analysis of the chemical contents of the shell offers better results in determining age]

POLYPLACOPHORA

SIRENKO, B. I.

1977. The vertical distribution of the chiton genus *Lepidopleurus* (Lepidopleuridae) and a new ultraabyssal species. ZZ 56 (7): 1107 - 1110 (ES)

[Known from the Carboniferous, *Lepidopleurus* is the most ancient of Recent chiton genera. It is characterized by a series of archaic features such as the weak development of the articulamentum, absence of insertion plates, narrow apophyses, and narrow muscular bands around the shell. Present in all seas except those with low salinity, *Lepidopleurus* is found mainly in the boreal regions, from the shallow zone to great depths. *Lepidoxona vityazi* is described from the Bugenvilsky Trench at 6920 - 7657 m and constitutes the most abyssal of known chitons]

STAROBOGATOV, YA. I. & B. I. SIRENKO

1975. On the systematics of the Polyplacophora. MN, Sb. 5, pp. 21 - 23

[The following classification is proposed: Subclass Paleoloricata with Order Chelodida, Suborder Chelodina (2 families) and Suborder Septemchitonina (1 family); Subclass Neoloricata with Order Scanochitonida, new (1 family), Order Lepidopleurida, Suborder Lepidopleurina (3 families), Suborder Chorioplacina, new (2 families), Order Chitonida, Suborder Tonicellina, new (6 families), Suborder Acanthochitonina (2 families) and Suborder Chitonina (4 families)]

GASTROPODA, GENERAL

DAMYANOV, SERAFIM G. & ILYA M. KOKHAREV

1975. The fauna of Bulgaria. 4. Land gastropods. Sofia, Bulgarian Acad. Sci., 425 pp.; illust.

[Included are 214 species and subspecies: 4 species in 2 families of prosobranchs, 3 species of one family of basommatophoran pulmonates, and 24 families of stylommatophorans. A thorough and varied introduction discusses numerous phases of the biology, physiology and ecology of these mollusks]

MINICHEV, YU. S. & YA. I. STAROBOGATOV

1975. On the systematics of the Euthyneura. MN, Sb. 5, pp. 8 - 11

[Four groups exist in the Euthyneura: 1) the Siphonariidae, which are possibly not related to primitive hyperstrophic forms; 2) the Pulmonata; 3) the typical opisthobranchs; and 4) the aberrant

opisthobranchs. The latter 3 groups are phylogenetically related to primitive hyperstrophic forms. The independent origin of these 4 groups from primitive Diotocardia is demonstrated and it is suggested that each group should be regarded as a subclass]

NAIDENKO, V. P. & T. KH. NAIDENKO

1976. Thermal stimulation of spawning and cultivation of larvae of two species of gastropods in aquaria. EEMB, pp. 125 - 126

[*Tectonatica janthostoma* and *Aeolis* sp. were induced to lay eggs; features of their reproductive biology are discussed]

PETRUYANKA, V. V.

1977. The distribution of carotenoids and myoglobin in the tissues of pulmonates. Zh. evolyuts. biokhimii i fiziol. 13 (2): 218 - 220 (ES)

[Tissue extracts of *Helix pomatia*, *Lymnaea stagnalis*, and *Planorbis cornutus* were studied spectrophotometrically]

SHILEIKO, A. A.

1975. Peculiarities of the excretory system of the pulmonates in connection with their subclass classification. MN, Sb. 5, pp. 12 - 15

[The structure of the kidneys is at present used as the major taxobasis for the classification of the Pulmonata. It is demonstrated that the sigmurethrous condition, in one form or another, appears in all terrestrial pulmonates, even in the Orthurethra. However, in that group, the distal portion of the kidney displays a tendency to be shorter. The heterurethrous condition is the first result of shell reduction in all groups where this reduction takes place. For these reasons the taxonomic distinction of larger groups on the basis of the kidneys is not feasible]

SIBER, L. S. & L. I. PSHENICHNIKOVA

1976. Melanistic pigmentation of some freshwater and terrestrial gastropods and its significance. Vopr. biol. i agronomii (Problems in biology and agronomy), Tomsk, pp. 100 - 106

[In aquatic pulmonates, aquatic prosobranchs and land pulmonates the pigmentation is without taxonomic significance, but, in some cases, may serve a thermo-regulatory function]

STAROBOGATOV, YA. I.

1977. Class Gastropoda [in] *Opredelitel' presnovod. bespozvonochnykh Evrop. chasti SSSR* (Handbook of freshwater invertebrates of the European portions of the USSR). Plankton and Benthos. Gidrometeoizdat, Leningrad, pp. 152 - 174

[58 species in 13 families of gastropods are considered; brief ecological notes, distributional data, and synonymies are provided]

STAROBOGATOV, YA. I. & L. L. BUDNIKOVA

1976. On the freshwater gastropod fauna of the extreme north-eastern USSR. DVBPI 36 (139): 72 - 88

[In total, 20 species are considered, 15 from the Chukotsk Peninsula; 4 species are common to America and the Chukotsk, 1 from northwestern America new to the USSR. 2 new species and 1 new subspecies are described]

YEVONIN, L. A. & YU. S. MINICHEV

1975. Adaptations of pelagic mollusks. MN, Sb. 5, pp. 24 - 26

[The basic adaptive change involved the organs of locomotion, and alterations of other structures are correlated with it]

PROSOBRANCHIA

CHUKHCHIN, V. D.

1976. The functional morphology of *Semisalsa dalmatica*, a gastropod new to the Black Sea. ZZ 55(11): 1627-1634

[*Semisalsa dalmatica* resembles the Hydrobiidae but differs in the morphology of its reproductive system. Unlike the hydrobiids, the pallial oviduct is a simple slit and does not have longitudinal folds separating it from the vaginal canal. The renal oviduct has 2 light [colored] loops and lacks the dark pigmented spiral of hydrobiids. A channel connects the oviduct with the mantle cavity. The male reproductive system also differs from that of the hydrobiids. Structurally, *Semisalsa* is a rissoid but not assignable to any known family. Although the female genital anatomy indicates a relationship with the Cingulopsidae, the male system differs decidedly. It is suggested that a separate family may have to be erected]

GALKIN, Yu. I.

1976. The distribution of Trochidae in the Barents Sea with contemporary changes of climate. Donnaya fauna Kraev. mor-yei SSSR (Benthic fauna of the regional seas of the USSR), pp. 61-77 (ES)

[Encompassing data from 1838-1973, there were changes in the Trochidae which corresponded with temperature variations. During the 1920's and 1930's, a warming of water drove the arctic species northward and allowed an increase in boreal species. A reversal of this process occurred during the period of chilling in the 1960's]

GONCHAROV, A. D.

1977. *Rapana* at the northwestern shore of the Black Sea. Gidrobiol. zh. 13 (3): 29-31

[Data are provided on the distribution, density, composition and distribution at various depths and substrates. A morphologically distinguishable form, *Rapana thomasi* *thomasi* *odessanus*, is established]

GORYACHEV, V. N.

1977. New data on the morphology and distribution of *Nepetunea laticosta* Golikov (Gastropoda, Buccinidae). ZZ 56 (4): 631-633 (ES)

[The egg capsule and the structure of the distal portion of the penis are described. The species is cited for the first time from the Bering Sea in the presence of the subspecies, *N. laticosta ochotensis*]

KARABELL, O. Z.

1977. The distribution of the species of *Abeskunus* in the central and southern Caspian. VINITI, Manuscript dept., No. 1959-77

[From 321 stations, more than 150 000 specimens of *Abeskunus* Kolesnikov, a subgenus of *Pseudamnicola*, were taken. Geographical, ecological, and bathymetrical data are provided for 3 species: *A. brusinianus* (Clessin & Dybowski) occurs from shallow depths to 210 m in all the central and southern Caspian; *A. sphaerion* (Mousson) is found mainly in the southern Caspian to depths of 50 m; and *A. depressispira* (Logvinenko & Starobogatov) is stenotopic in the southern Caspian to 100 m]

KARABELL, O. Z. & B. M. LOGVINENKO

1977. The distribution of the gastropods of the section of *Trachycaspi* of the genus *Turris* in the central and southern Caspian Sea. VINITI, Manuscript dept., No. 559-77

[Three species of *Trachycaspi* are now known. The most widely distributed and abundant species, *T. dimidiata* Eichwald, is found mostly in the central part of the sea although a few occur to the south in the Apsherenki Rapids and occupy widely differing substrates, mainly between 10-250 m. *T. bakuana* Kolesnikov, endemic in the southeastern Caspian, lives to 100 m in substrates different from the other species. *T. laticarinata* Logvinenko & Starobogatov, endemic in the southwestern Caspian to depths of 160 m, has narrow ecological tolerances and a restricted geographic range. All these species have patchy distributions within their ranges, a situation possibly correlated with the absence of a swimming larva]

KONDRATENKO, A. P.

1976. Potential tolerance to salinity in populations of *Hydrobia* from the White Sea. EEMB, 87-89

[After acclimatization to an initial salinity of 20 parts per 1000, the euryhalinity of the mollusks increased an average of 4.5 times. The potential tolerance of various populations differs strongly and increases from the open sea toward estuaries]

LUS, V. YA

1976. New and rare deepsea buccinid species from the Kuril-Kamchatka and Japanese Trenches. TRO 99: 71-84 (ES)

[*Buccinum lamelliferum* is described as new from the Kuril-Kamchatka Trench. Additional data on abyssal and bathyal species, *B. diplosetum* Dall, 1907 and *B. kashimanum* Okutani, 1964, are provided. The shell, operculum, radula and anatomy of each species are discussed]

MATVEEVA, T. A.

1977. The reproductive ecology of several species of gastropods in the upper shelf of the Sea of Japan Shelf (Pos'teta Bay). 1. S'ezd sov. okeanologov, vyp. 2, tezis dokl., Moscow, "Nauka," (First session of soviet oceanologists, 2. thesis reports), pp. 24-25

[The following types of larval development were observed:

1) Pelagic

- a) the veliger develops from a free swimming trochophore: (*Collisella radiata*, *C. heroldi*);
 - b) the veliger develops in a planktonic egg capsule (*Littorina brevicula*, *L. squalina*, *Tegula rustica*);
 - c) the veliger develops inside the deposited egg-case which is fastened to a firm substrate (*Ephera turrita*, *Thapsiella plicosa*, *Tectonatica janthostoma*, *Boreotrophon candelabrum*, *Mitrella burchardi*, *Nucella heysiana*, *Tritia* sp.);
- 2) Direct development - the veliger develops in the deposited egg which is fastened to the substrate (*Littorina kurila*, *Falsicungula mundana*, *Euspira pila*, *Tritonalis japonica*, *Tritia acutidentata*, *Homalopoma sangarens*).

Larvae appear in the plankton at the end of March at a water temperature of -0.7°C and a relative scarcity of phytoplankton. In May, the number of larvae increases considerably and reaches the maximum in June. In the following months the numbers decrease gradually and in October only isolated individuals are seen in the plankton. The settling of the larvae and the appearance of young in most species takes place from July to September. This later phase of reproduction is limited by rather narrow temperature limits (18-21°C)

MOSKALEV, L. I.

1976. On the generic classification of the Cocculinidae (Gastropoda; Prosobranchia). TRO 90: 59-70 (ES)

[6 new genera and their type-species are described: *Fedikovella* (*F. caymanensis*), *Teuthirostia* (*T. cancellata*), *Kurilabyssia* (*K. squamosa*), *Caymanabyssia* (*C. spina*), *Bandabyssia* (*B. costocentrica*), and *Tentaoculus* (*T. perlucida*). 69 species and 2 genera previously described are listed]

PAKHOMOV, A. N.

1976. An analysis of deviation and regulation of the distribution of isozymes in *Littorina littorea* during the adaptation to salinity fluctuations. EEMB, pp. 137 - 138

POBEREZHNYI, E. S. & T. YA. SITNIKOVA

1976. A report on the number of chromosomes of the Lake Baical species *Benedictia baicalensis* Gerstf. (Gastropoda, Prosobranchia). Novy materialy po faune i flore Baikala, Irkutsk, pp. 142 - 144

[2N = 34 with 17 bivalents at metaphase]

SHILEIKO, A. A.

1977. The symmetry of the Docoglossa and the problem of the origin of the order. Byul. Mosk. O-va ispyt. prirody Otd. Biol. (Bulletin of the Moscow Naturalist's Society, Biology Series) 81 (3): 60 - 65 (ES)

[The representatives of the Docoglossa have neither a turbospiral form nor stage in their ontogenesis. The asymmetry of the mantle cavity is therefore not related to a former turbospiral stage but to the adaptation of the respiratory system to aquatic currents; these adaptations include the disappearance of the right ctenidium and the concomitant restructuring of internal organization. Thus, the symmetry of the Docoglossa is a primitive feature and the shell is initially exogastric. Earlier endogastric ancestors might well have been the Cambrian Helcionellidae]

SIRENKO, B. I. & V. L. KAS'YANOV

1976. The abalones of Monneron Island (Sea of Japan). Biol. Morya, No. 6, pp. 20 - 25 (ES)

[The authors claim that the presence of *Haliotis kamtschatkana* in the seas of the USSR is based on erroneous 19th century labels. The northernmost Soviet population of *Haliotis discus* occurs on Monneron Island and some biological details of this population are provided]

TSIKHON-LUKANINA, E. A.

1976. The feeding of the gastropod *Gibbula divaricata* in the littoral zone of the Black Sea. EEMB, pp. 186 - 188

[A study of the energy flow in colonies of *G. divaricata* which feed on periphyton and detritus]

VILENKIN, B. YA. & M. N. VILENKINA

1977. Response of individuals of White Sea populations of *Littorina obtusata* and *L. littorea* to temperature changes. ZZ 56 (6): 829 - 834 (ES)

[Individuals of the 2 species of snails were placed into artificially controlled temperature regimes and showed differences in preferences. Homing was clearly observed in *L. littorea* but less so in *L. obtusata*, a phenomenon which apparently correlates with the pelagic larva of the former and the direct development from the egg of the latter. Being panmictic, *L. littorea* apparently is characterized by a more greatly developed system of acclimatizations]

OPISTHOBRANCHIA

MINICHEV, YU. S.

1976. On the morphology of the pelagic mollusks of the family Pneumodermatidae (Opisthobranchia, Gymnosomata) in Antarctic waters. IFML 18 (26): 102 - 106 (ES)

[A discussion of the characteristics of the Pneumodermatidae is provided and *Platybrachium antarcticum* (a new genus and new species) and *Pneumodermopsis brachialis* (a new species) are described]

1977. On the morphology and systematics of the genus *Cylichna* (Gastropoda; Opisthobranchia) from Franz-Josef Land. IFML 14 (22): 428 - 434 (ES)

[*Cylichna occulta* (Mighels), *C. alba* (Brown), and *C. arctica* (a new species) are described. A new subgenus *Cylichnoides* is erected on the basis of shell structure and reproductive morphology with *C. occulta* as type species. The subgenus possesses a different copulatory apparatus and a lamellar larval shell. The peculiarities of heterostrophy are noted for several species]

TERRESTRIAL PULMONATA

AKRAMOVSKI, N. N. & G. S. BABAYAN

1976. Methods in controlling the mountain snail (*Vitrinoides monticola armenica*) against attacking hothouse tobacco in Armenia. Tekhekagir gyukhatntesakan gitutyunner, Izv. s.-kh. Nauk, No. 10, pp. 68 - 72 (Armenian with Russian summary)

[The snail is nocturnal in its habits; chemicals and their applications against these pests are discussed]

BURENKOV, M. S.

1977. The growth structure of populations of 3 species of snails *Stylommatophora*, Pulmonata. ZOB 38 (2): 296 - 304 (ES)

[Populations of *Agriolimax reticulatus*, *A. laevis* and *Arion circumstrictus* were studied in different biotopes; the number of generations per annum is correlated with climate, being least in the most rigorous conditions and most in the more equitable]

DMITRIEVA, E. F. & YA. S. SHAPIRO

1976. Physiological and toxicological aspects in the postembryogenesis of the reticulated slug (*Agriolimax reticulatus*). Nauchnye trudy Leningrads. s.-kh. in-ta. 297: 91 - 94

GOROKHOV, V. V., A. A. SHILEIKO & R. YA. BUTYLIN

1975. On the terrestrial molluscan fauna as intermediate host of protostrongilids in southern Kirgizia. Tr. vses. in-ta helmintol (Transactions of the All Union Institute of Helminthology) 22: 43 - 51 (ES)

[52 species are found in the pasturelands. 3 epidemiological situations are recognized: 1) a dangerous zone in the spring, fall and winter pasturelands at 1000-2000 m above sea level where, basically, invading animals with protostrongilids originate; 2) a potentially dangerous zone in summer pasture lands at 2000-3000 m where sheep with protostrongilids appear to a lesser degree; 3) on summer

pasture land at 3000m and higher where sheep infected with protostrongilids do not appear]

KHOKHUTKIN, I. M.

1976. Polymorphism as a method in determining populational areas of land mollusks. SPZM, pp. 153 - 154

[The polymorphic structure may serve as a criterion for the continuity of distributional areas of a species]

KHOKHUTIN, I. M. & A. I. LAZAREVA

1975. Polymorphism in populations of some Caucasian land mollusks. Mn, Sb. 5, pp. 32 - 34

[The banding structure of populations of *Fruticocampylaea naranensis*, *Xeropicta krynickii*, and *Caucasotachea atrolabiata* was studied. It was shown that, unlike dimorphic populations of *Bradybaena*, the polymorphism of the populations studied is phenotypic in nature]

LIKHAREV, I. M.

1975. The zoogeographic characteristics of the land molluscan fauna of Bulgaria and its origin. MN, Sb. 5, pp. 26 - 29

[There are 9 zoogeographical groups: 1) widely distributed, boreal species (23); 2) general European species (34); 3) Euxine species (18); 4) Atlantic-Mediterranean species (7); 5) Southern European mountain species (10); 6) Central European mountain species (26); 7) endemic Balkan species and subspecies (50); 8) xerophilic species of Near-Eastern origin (16); and 9) xerophilic species of Mediterranean origin (13). In the fauna of the Balkan Province, almost half of the 550 species are endemic]

MUKHITDINOV, A. B.

1975. Zoogeographical analysis of the land mollusks of North Tajikistan. MN, Sb. 5, pp. 29 - 31

[Of the 63 species (26 genera and 13 families), 3 zoogeographical groups can be recognized: 1) widely distributed boreal species (10); 2) Euro-Asiatic mountain species (7); 3) endemic northern Asian species (41)]

NIKOLAEV, V. A.

1976. On the ecology and distribution of helicoids in the heights of central Russia. SPZM, pp. 109 - 111

[7 species of helicoids are known from there in the families Hydrobiidae and Helicidae. Short remarks on their distribution and ecology are included]

OMAROV, ZH. K. & A. F. IVAN'KOVA

1976. Double diffusion reaction in starch-gel immunochemical analysis of the polymorphic species *Bradybaena plectotropis*. KazSSR Fylym Akad. Khabalary, Izv. AN KazSSR, Ser. Biol. 4: 18 - 24 (Kazakh summary)

[Antigenic studies confirm the large degree of polymorphism of *B. plectotropis* in comparison to *B. lantzi*]

PAKHORUKOVA, L. V. & P. V. MATEKIN

1977. Interspecific distinctions in the influence of temperature on the duration of embryonic development in slugs. ZOB 38 (1): 116 - 122 (ES)

[A comparison of geographically separate populations of *Agriolimax agrestis* and *A. reticulatus* showed decided differences in the influence of temperature on the length of embryogenesis]

PIROGOV, V. V.

1977. The terrestrial pulmonate fauna of the Volga Delta. ZZ 56 (8): 1248 - 1250 (ES)

[7 species of stylommatophorans were taken, of which *Succinea elegans* (Risso), *Pseudotrachia rubiginosa* (A. Schmidt) and *Zonitoides nitidus* (Müller) were most numerous, sometimes occurring in densities of 2500/m². Spring floods control the densities and effect dispersal]

REZNIK, Z. V.

1976. Faunistic characteristics of land mollusks in the flood plain forests of the Kuma River. SPZM, pp. 131 - 133

[There is a decline in the number of species in forests along the Kuma from the border of Georgievskaya to the village of Vladimirovka]

SHAPIRO, YA. S.

1976. Harmful slugs. Zashchita rastenii (The Protection of Plants), No. 9, pp. 28 - 30

[Data on the external structure and the biology of the most common species in the USSR are provided]

SHIKOV, E. V.

1976. On the dispersal of land mollusks during flood times. ZZ 56 (3): 361 - 367 (ES)

[28 species of slugs and snails, constituting 57% of the malacofauna of the Kalinin region are transported by flood waters. The extent of this dissemination depends on the geomorphology of the terrain and on the nature of the animals]

SOKOLOV, V. A. & V. A. KOVALEV

1977. The electrical activity of the cerebral ganglia of *Helix vulgaris* during statocyst stimulation. Zh. evolyuts. biokhimi i fiziol. 13 (4): 512 - 513 (ES)

[Testing was conducted at 30, 60, 150, 300, 500, and 1000 Hertz. Since at frequencies of 2000 and 5000 there was no response, the threshold frequencies were established at a low of 30 and a high of 1000. 3 - 4 stimulations at one frequency at intervals from 1 - 2 minutes brought about a reduction and finally a disappearance of a response. Transference to another frequency occasioned renewal of the response. The neuronal cells associated with the statocyst stimulate a response in the cerebral ganglia]

PULMONATA, AQUATIC

ARUTYUNOVA, L. D.

1977. Aphallia in a population of *Radix* (Gastropoda, Lymnaeidae) from Armenia. Biol. Zhur. Armenii 30 (3): 89 - 90 (Armenian summary)

[50% of a population of *Radix auricularia* in the plain of Ararat was found to be aphallic. The mollusks were not infected, and the condition was not due to parasitological castration]

GUSEVA, M. I.

1976. On the general problem of the pasture malacofauna in the Irkutsk region. Trudy Irkutskoi Nauchno-issledovatel'skoi Veterinarnoi Opytnoi Stantsii (Works of the Irkutsk Experimental Station for Veterinary Studies), Vyp. 3, pp. 280 - 282

[8 species in 3 families of freshwater pulmonates were found in 20 pastoral areas]

KRUGLOV, N. D.

1976. Perspectives on the utilization of an experimental method of hybridization in the systematics of the lymnaeids. SPZM, pp. 78 - 79

[General observations on the functions of portions of the reproductive tract in *Lymnaea corviformis*]

LEVINA, O. V.

1975. Seasonal dynamics of size-age structure in some lymnaeid populations. MN, Sb. 5, pp. 86 - 88

[In the Kiev Reservoir in 1971, the maximum growth in populations of *Lymnaea stagnalis* and *L. ovata* occurred in August]

MASARONOVSKI, A. G. & M. I. GUSEVA

1976. On the features of the biotopes of small pond snails in the pasture areas of the Irkutsk region. Trudy Irkutskoi Nauchno-issledovatel'skoi Veterinarnoi Opytnoi Stantsii (Works of the Irkutsk Experimental Station for Veterinary Studies), Vyp. 3, pp. 277 - 279

[Natural conditions favor fewer lymnaeids and thus decrease the incidence of fasciolariasis]

NEIFAKH, A. A.

1976. On the morphological function of the nucleus in the early development of *Lymnaea stagnalis*. Ontogenez 7 (6): 630 - 633 (ES)

[Experiments are described which utilize the inhibitory effect of actinomycin on the early developmental stages in *Lymnaea*]

SOKOLOV, V. A. & N. N. KAMARDIN

1977. Impulse frequency in the osphradial nerve of lymnaeid pond snails under varying osmotic conditions and different concentrations of oxygen. Vestn. Leningrad. Univ. 3: 87 - 90 (ES)

STAROBOGATOV, YA. I.

1976. On the composition and systematic placement of marine pulmonates. Biol. Morya, No. 4, pp. 7 - 16 (ES)

[Several groups of mollusks which differ phylogenetically are assigned to the primitive pulmonates. These are the orders Ellobiida, Amphibolida, and Trimusculida. In the Ellobiida, 4 superfamilies can be distinguished: 1) Subulitoidea including Subulitidae Lindstrom, 1884 and Soleniceidae Wenz, 1938; 2) Melampodoidea, including Melampodidae Stimpson, 1851 and Otinidae H. & A. Adams, 1855; 3) Carychioidae including Carychiidae Jeffreys, 1829, Pythiidae Odhner, 1925, Anthracopidae Wenz, 1938, Velainellidae Vasseur, 1880, Zaptichidae Zilch, 1959, Pedipedidae Crosse & Fischer, 1880, and Cassidulidae Odhner, 1925; 4) Ellobioidea with the families Ellobiidae H. & A. Adams, 1885 and Leucophytidae (a new family). The order Amphibolida contains the families Amphibolidae Gray, 1840 and Salinatoridae Starobogatov, 1970. In the order Trimusculida, there is only the single family Trimusculidae Habe, 1958.

These orders of lower pulmonates, derived from primitive stylomatophorans, can be traced in the degrees of their adaptation to aquatic habitats. The families Onchidiidae and Rhodopidae, customarily included in the Pulmonata have no relationship to that subclass and they should be placed in the subclass Dextrobranchia and elevated in rank. In the order Rhodopida, only the family Rhodopidae Thiele, 1931 is included; the order Onchidiida has 3 superfamilies: Onchidelloidea, Onchidioidea, and Hoffmannoloidea. In the Onchidelloidea are included the Onchidellidae E. & E. Marcus, 1960, the Onchidinidae (a new family) and Peroninidae (also a new family); in the Onchidioidea there are the families Onchidiidae Rafinesque, 1815, Peroniidae Labbe, 1934, Platevindecidae (a new family) and Quoyellidae (another new family). Only the single new family Hoffmannolidae represents the Hoffmannoloidea.

Similarly, the Siphonariidae cannot be assigned to the Pulmonata and constitute another subclass, the Divasibbranchia with the single order Siphonariida and 2 superfamilies: 1) Siphonarioidea with the families Siphonariidae Gray, 1840, Anisomonidae (a new family), and Siphonacmeidae (another new family); and 2) the Rhytidophiloidea with the single new family Rhytidophilidae. The Siphonariida are distinguished from marine pulmonates which doubtlessly derived from primitive aquatic animals]

TATARYUNAS, A. B.

1976. Carotinoid content in the brain of *Lymnaea stagnalis* as determined by its physiological state. Obmen i funktsii vitamina A i karotina v organizme cheloveka i zhivotnykh, ikh prakt. ispol'z (Exchange and function of vitamin A and carotin in the human organism and animals, their practical use). Tezisy doklad. II. Vses. konf., Chernovits, pp. 152 - 153

BIVALVIA

ALYAKRINSKAYA, I. O.

1977. On the dissolution of the crystalline style in some bivalves. ZZ 56 (1): 23 - 27 (ES)

[Unfavorable respiratory conditions bring about a striking dissolution of the crystalline style in *Mytilus galloprovincialis* and *Cardium edule*; *Donax julianae* and *Mya arenaria* were unaffected]

1977. The adaptation of littoral White Sea bivalves to desiccation. ZZ 56 (7): 1110 - 1112 (ES)

[In *Macoma balthica*, calcium compounds in the shell are utilized to buffer the hemolymph while in *Mytilus edulis* the dissolution of the crystalline style takes place]

DZYUBA, S. M. & M. N. GRUZOVA

1976. Seasonal changes in RNA synthesis and morphology of female gonads in shallow water scallops. Biol. Morya, No. 4, pp. 38 - 44 (ES)

[The sexual cycle of *Patinopecten yessoensis* is divisible into stages including complete sexual inertia where there is no RNA synthesis in gonadal tissue during the winter, an active period of gametogenesis including the growth and maturation of the oocyte and, finally, the act of spawning the oocyte itself]

FILATOVA, Z. A.

1976. Monograph on the deepsea bivalve genus *Spinula* (Dall, 1908) (Malletiidae) and its distribution in the Pacific Ocean. TRO 99: 219 - 240 (ES)

[10 species, including *S. knudseni* and *S. thorsoni* described as new, are known. The genus occurs in the Pacific, Indian and Atlantic oceans and is notably absent from the Polar Basin and the Antarctic]

FLUSOVA, G. D. & T. I. BASHUROVA

1976. Polymorphism in the scallop *Patinopecten yessoensis* in the bays of the southern and central maritime province. Vses. konf. molodykh uchenykh nuach.-tekhn. progress v ryb. prom-sti (All-union conference of young students in scientific technical progress in the fishing industry), Moscow, pp. 12 - 13

[Populations from 8 bays were studied. A hypothesis is proposed regarding the multiple allelic system for esterase of the digestive diverticula in this species]

GOROMOSOVA, S. A. & A. Z. SHAPIRO

1977. Features of energy exchange of mussels in connection with their ecology. 1. S'ezd sov. okeanologov, vyp. 2, tezisy dokl. Moscow, Nauka (First session of soviet oceanologists, 2, thesis reports), p. 121

[Environmental stresses affect the rate of glycolysis in mussels]

IGNAT'EV, A. V. & E. S. KRASNOV

1976. Investigation of the effect of temperature on growth increments in the shells of scallops using isotopes of oxygen. Biol. Morya, No. 5, pp. 62 - 78 (ES)

[Measurements of isotopes of oxygen (O^{18}/O^{16}) were employed in studying growth layers in the shells of *Patinopecten yessoensis*, *Chlamys swifti* and *Ch. farrei nipponensis*. The dynamics of growth were correlated with seasonal parameters, such as temperature]

IGNAT'EV, A. V., E. V. KRASNOV & I. M. ROMANENKO

1976. The correlation between the magnesium content of mussel shells, their growth temperatures, mineralogical composition and age. EEMB, pp. 85 - 86

[Positively correlated with a rise in temperature, the magnesium content of growth layers of the shell varies ontogenetically and seasonally. In early years the average magnesium content in calcite in the shells of *Crenomytilus grayanus* is 0.08 to 0.1%; at about 70 years it rises to 0.15%]

KANDYUK, R. P., T. A. PETKEVICH, I. A. STEPANYUK, T. P. GROBY-LEVA & L. N. SHCHERBINA

1977. Some biochemical indices of Black Sea mollusks. Gidrobiol. Zh. 13 (1): 97 - 102

[In an analysis of trace elements and amino acids, different chemical compositions were noted in *Mytilus galloprovincialis*, *Ostrea taurica* and *Mya arenaria* in the northwestern part of the Black Sea]

KARTAVTSEV, YU. F. & S. M. NIKIFOROV

1976. Comparisons of some data on the morphology, physiology, histology, and biochemistry of *Crenomytilus grayanus* (Dunker) in order to determine its taxonomic status more accurately. Biol. Morya, No. 6, pp. 13 - 19 (ES)

[2 sympatric forms of *C. grayanus* were said to occur in Peter the Great Bay. The data examined do not justify the division into 2 independent species despite certain observed conchological differences in shell length and obesity]

KAZAKOV, V. K.

1977. On insulin-like materials in cells of the intestinal epithelium of *Unio pictorum*. Zh. evolyuts. biokhimi i fiziol. 13 (4): 439 - 442 (ES)

[Mammalian insulin-antiserum give an immunological reaction with midgut epithelia cells of *U. pictorum*]

KONOVALOVA, I. V.

1976. Data on the gradual development of early mid-Jurassic *Inoceramus* in southern Sikhotealinia. DVBPI 38 (141): 28 - 33 (ES)

[Morphological changes of the shell and ligamental apparatus were observed and 4 stages were discerned]

KUTISHCHEV, A. A.

1976. Characteristic selectivity by larval *Crenomytilus grayanus* (Dunker) before settling on the substrate. Dokl. AN SSSR 230 (3): 737 - 740

[Larvae actively search for a byssus secreted by mature individuals

of the same species, distinguish these byssi from other mytilids and other substrates, and eventually settle. Thus, it is the mature individuals which shelter the young in their byssal network which acts like a 'kindergarden' where the young generation is protected from predators]

MAMED'YAROVA, G. M.

1976. On the systematics of the family Apscheroniidae Sultanov. VPS, Vyp. I, pp. 134 - 140

[The group has a monophyletic origin, deriving from various species of the genus *Cardium*. The following arrangement is proposed: Superfamily Cardiacea; Family Apscheroniidae; Genera *Parascheronia*, 5 species; *Apscheronia*, 4 species]

MARGULIS, B. A. & G. P. PINAEV

1977. The differences in the composition and nature of the albumen from the adductor muscles of bivalves. Biol. Morya No. 1, pp. 63 - 72 (ES)

[In 26 species of bivalves, disc-jel electrophoretic analysis of muscle fibers and albumens revealed differences consonant with taxonomic distinctions, especially at the generic and familial levels]

MATVEEVA, T. A.

1976. The biology of the bivalve *Turtonia minuta* in different parts of its range. Biol. Morya, No. 6, pp. 33 - 39 (ES)

[Data are presented regarding the habitat, depth, population structure, and the time of spawning. Also the systematic placement of this species is examined]

1977. Reproduction in bivalves of the family Astartidae. IF ML 14 (22): 418 - 427 (ES)

[*Tridonta borealis* (Schumacher), *T. montagui* (Hancock), and *Astarte elliptica* (Brown) have a wide distribution in arctic and sub-arctic waters. They are characterized by a long period of gametogenesis but a short spawning period in autumn and winter. Eggs are large (300 μ m), yolky and enveloped by 2 jelly-like membranes which promote swelling and stickiness after fertilization. Growth takes place relatively rapidly. Protandric hermaphrodites, the Astartidae have populations with large-sized females which increase fecundity and reproductive effectiveness]

MATVEEVA, T. A. & N. V. MAKSIMOVICH

1977. Characteristics of the ecology and distribution of *Hiatella arctica* (Heterodonta) in the White Sea. ZZ 56 (2): 199 - 204 (ES)

[Preferring hard substrates, the species is widely distributed and eurybiontic, living mostly in depths between 5 and 10 m, but occasionally to 60 m. It matures sexually at the end of its first year when it reaches a length of about 14 mm. Spawning takes place in June-July and the larvae settle by October. Winter mortality is highest in young of the year. With shells measuring up to 31 mm in length, the species may live as long as 6 years]

MILOSLAVSKAYA, N. M.

1977. Mollusks of the family Thyasiridae (Bivalvia, Lucinoidae [sic] of the Arctic seas of the USSR. IFML 14 (22): 391 - 417 (ES)

[The Arctic Thyasiridae consist of 3 genera and 8 species, one of which (*T. phrygiana*) is described as new. Detailed descriptions, a dichotomous key, ecological comments, and an analysis of zoogeographic distribution are provided]

MIRONOV, O. G. & T. L. SHCHEKATURINA

1977. On the hydrocarbon composition of *Mytilus galloprovincialis* in the Black Sea. ZZ 56 (8): 1250 - 1256

[In the Black Sea, these mussels may be indicators of oil pollution inasmuch as they show a considerable uptake of hydrocarbons, including n-paraffins]

NAIDENKO, T. KH. & N. I. SELIN

1976. On the survival rate of young *Patinopecten yessoensis* on various types of substrates. EEMB, pp. 132 - 134

[The accumulation of sand is a less favorable bottom for the settling and survival of this scallop than that of sand with an admixture of shells]

NAUMOV, A. D.

1977. The influence of rising temperatures on *Portlandia arc-tica* from two different populations in the White Sea. Biol. Morya, No. 2, pp. 74 - 77 (ES)

[Populations from conditions where the temperature is constantly below 0°C are less able to adjust to increased temperatures than those individuals from shallow water where summer temperatures rise to 2.5°C. These differences are not sufficient to regard the different populations as distinct physiological races]

NISTRATOVA, S. N.

1976. The connection between the life cycle of mollusks and the sensitivity of cardiac muscle to acetylcholine. EEMB, pp. 135 - 136

[There is a correlation between the increase of sensitivity to acetylcholine and the maturation of the gonads]

PRYADKO, V. P.

1976. Observations on calcium exchange in the tissues of *Anodonta cygnea* L. Dokl. AN SSSR B, No. 9, pp. 833 - 837 (ES)

[Calcium was found in all tissues, though differential concentration in the mantle was noted]

RODIONOV, V. F., E. D. PAVLOVA & M. N. ZATRAVKIN

1976. The mollusks of Lake Seliger. SPZM, pp. 133 - 134

[21 species of Unionidae and Sphaeriidae were found]

SABUROV, E. G.

1976. Diurnal dynamics of the movement of the mantle fold in *Anodonta cygnea* in varying water conditions. Sravnit. issled. izmenenii fiziol. funktsii pod vliyaniem estestv. i sintetich. detergents (A comparative study of the change of physiological function under the influence of natural and synthetic detergents). Yaroslavl', pp. 64 - 67

SAVCHUK, M. YA.

1976. The acclimatization of *Mya arenaria* in the Black Sea. Biol. Morya, No. 6, pp. 40 - 46 (ES)

[First reported in 1966, *M. arenaria* has now generated a new biocenose in the Black Sea. In places it reaches a density of 2000 spm per m² and a biomass of 10 kg/m². Attaining a length of 92 mm, the species may become commercially important]

SHUST, I. V., I. M. KOSTINIK & L. G. KUZ'MOVICH

1976. Morphohistochemical characteristics of the sexual organs of *Anodonta piscinalis* Nilss. SPZM, pp. 170 - 172

SKARLATO, O. A. & YA. I. STAROBOGATOV

1975. New data for constructing a system of Bivalvia. MN, Sb. 5, pp. 4 - 8

[Modifications are suggested for the improvement of the systematic scheme of the Bivalvia as proposed by Nevesskaya, Scarlato, Starobogatov and Eberzin in 1971]

SKUL'SKI, I. A.

1976. On the role of calcium in the adaptation of a marine mollusk to low environmental salinities. EEMB, pp. 165 - 166

[In *Mytilus edulis*, calcium is important for: the maintenance of is-osmotic pressure, the creation of membrane potentials, the activity of certain enzymes, and the neutralization of negative charges in cells]

SOKOLOV, V. A.

1977. Cerebral influence on the visceral ganglia via the circum-pallial nerve in *Unio pictorum* (Linn.). Vestn. Leningr. Univ., No. 9, pp. 85 - 88 (ES)

[This neurophysiological study shows how nerve impulses from the cerebral ganglia can reach and affect the visceral ganglia via the circumpallial nerve in addition to the more usual path via the cerebro-visceral connectives]

STAROBOGATOV, YA. I.

1977. Mollusca, Class Bivalvia [in] Opredelitel' presnovod. bespozvonochnykh Evrop. chasti SSSR (Handbook of the freshwater invertebrates of the European portions of the USSR). Plankton and Benthos. Gidrometeoizdat, Leningrad, pp. 123 - 151

[57 species in 4 families of bivalves are considered; brief ecological notes, distributional data, and synonymies are provided]

TSIKHON-LUKAPINA, E. A. & T. A. LUKASHEVA

1975. Feeding of the shipworm *Teredo navalis*. MN, Sb. 5, 140 - 142

[A résumé of laboratory experiments]

VARAKSIN, A. A.

1976. Neurosecretory activity of cerebropleural ganglionic neurons in the gametogenesis of the mussel *Crenomytilus grayanus*. EEMB, pp. 39 - 42

[The functional physiological condition of the nervous elements of the ganglia is closely correlated with the reproductive cycle]

1976. The neuroendocrine cycle and regulation of gametogenesis in the Bivalvia. EEMB, pp. 43 - 45

[*Crenomytilus grayanus* and *Patinopecten yessoensis* were examined morphologically, morphometrically, and electronmicroscopically. The physiological neuroendocrine activity depends on ecological factors - partly on the water temperature. The physiological mechanisms by means of which the ecological factors influence the condition of the neuroendocrine system are unclear]

1976. On the neurosecretions of the marine bivalves *Crenomytilus grayanus* (Dunkér) and *Patinopecten yessoensis* (Jay). Materialy VII mezhdunarod. simpoz. po neurosekretnii evolyuts. aspekty neuroendokrina (Data of the 7th international symposium on neurosecretion in evolutionary neuroendocrin aspects), Leningrad, p. 165

[A decrease of the average parameters of the nucleus and the body of neurons of the cerebropleural, visceral, and pedal ganglia was observed at the time of sexual inactivity. Ecological factors, which condition gametogenesis and spawning, are affected by the nervous

system. It is surmised that control over gametogenesis and spawning can be accomplished by neuroendocrines]

VASIL'eva, V. S.

1976. Seasonal changes in the heat resistance of the cells of the filtering epithelium of the ctenidia of *Crenomytilus grayanus*. EEMB, pp. 46 - 47

[The changes are not adaptations to the absolute temperature of the water; rather, they decline at the same time as the activity of the sexual and neurosecretory apparatus declines]

VEKILOV, B. G., E. M. ASADULLAEV & S. K. KARYAGDY

1976. Brackish water anthropogenic representatives of the genus *Didacna* Eichwald in Azerbaijan. VPS, Vyp. I, pp. 10-22

[A short survey of the group. A summary of published data together with personal investigations show the presence of 55 species of the genus in anthropogenic deposits. Stratigraphic analyses show the principal significance of the representatives of the genus]

VIGMAN, E. P.

1977. On the role of age structure in the maintenance of the stability of the glands [gonads] of *Crenomytilus grayanus* (Dunker). Dokl. AN SSSR 234 (5): 1222 - 1225

[A study of the production of larvae of this species indicates that a certain level of constancy may be maintained and that the species may be especially fit for aquaculture]

ZAİKO, N. N.

1976. The dynamics of the chlorine content in the growth layers of marine bivalve shells in connection with the saline conditions of their habitats. EEMB, pp. 73 - 74

[Chlorine ions are incorporated into layers of the shell and the rate is correlated seasonally]

ZAİKO, N. N., E. V. KRASNOV & O. I. NEDAVA

1976. On the determination of the salinity of ancient marine bodies of water by study of the chemical content of molluscan shells. Biol. Morya, No. 6, pp. 61 - 63 (ES)

[In an examination of 11 shells of Recent and Neogene-Quaternary specimens of *Arctica islandica*, the method of Raker and Valentine, with modification proposed by Zakharov and Radostev, was shown to be satisfactory]

CEPHALOPODA

BARSKOV, I. S.

1975. Shell structure and the evolution of the ontogenesis of the cephalopods. MN, Sb. 5, pp. 171 - 173

[The development of a decidedly late embryonic shell coupled with the simultaneous appearance of 4 gills is an early evolutionary acquisition and possibly represents the most primitive state in cephalopod evolution. Bactrids and orthocerids (e.g., ammonites) have a comparable structure in the early portions of their straight shells, which apparently reflects their incomplete metamorphosis and veliger-like larvae]

DURSHITS, V. V.

1976. The structure of the shell of ammonites and its ontogenetic stages revealed by electron microscopy. EEMB, pp. 57 - 60

[The investigation indicated that ammonites exhibit direct development]

GAEVSKAYA, A. V. & CH. M. NIGMATULLIN

1976. Biotic relationships of *Ommastrephes bartrami* in the northern and southern parts of the Atlantic Ocean. ZZ 55 (12): 1800 - 1810 (ES)

[A helminthological investigation in which new representatives of didimozoid metacercaria are reported in *Ommastrephes*]

KRIVOSHAPKINA, V. S.

1976. On the ontogenesis of the suture line of *Zelandites*. DV BPI 38 (141): 72 - 78 (ES)

[In this, the first study of the change in the suture line of *Zelandites*, a close resemblance is noted to *Gaudryceras* and *Eogaudryceras* of the subfamily Gaudryceratinae, which supports Vidman's supposition that *Zelandites* was derived from *Eogaudryceras*]

NESIS, K. N.

1975. A comparison of the cephalopod fauna from both coasts of Central America. MN, Sb. 5, pp. 156 - 158

[The deep water faunas of the Eastern Pacific (EP) and the Inner American seas (IA = Caribbean Sea, Gulf of Mexico and adjacent bodies of water) have been isolated for not less than 10 to 15 million years and the surface, sublittoral faunas for not less than 4 to 5 million years. The number of benthic and oceanic species of both areas is quite similar while the nekto-benthic, benthic-pelagic and nerito-oceanic species in the EP are sharply impoverished in comparison with the IA. It is possible that the EP tropical fauna was reduced in the Pleistocene as a result of changes in the water currents]

1975. The ecological evolution of the cephalopods. MN, Sb. 5, pp. 152 - 155

[Recent cephalopods evolved along 3 basic lines: nektonic, nekto-benthic, and benthic. Evolution and specialization did not occur as a result of the widening or narrowing of the initial adaptive zone, but rather by transfer to different zones. Mainly, evolution took place on the tropical shelf in a struggle with other organisms such as fish, and, principally, organs of locomotion were subjected to the most intense selection pressure in attempting to secure this favorable, vital habitat]

1977. The biology of *Argonauta boettgeri* and *A. hians* in the Western Pacific and the Malay Archipelago. ZZ 56 (7): 1004-1014 (ES)

[The distribution and biology of both species are similar; *A. boettgeri* occurs mainly in the North Equatorial Current and its branches while *A. hians* is found around Flores, Banda and Halma-hera. The males mature before their mantle reaches about 7 mm and die after the first mating. The females mature when the mantle is about 15 mm and they prolong the time of their growth and reproduction. The length of the mantle and the shell of the female are compared. It is hypothesized that incubation extends for 3 days, and that the female deposits some eggs in the shell and expels a group of larvae every night. The female is a specialized pelagic organism and feeds on pteropods and heteropods. Possibly they feed during the day in subsurface waters. At night, the female prefers to attach herself to living or non-living objects which float or drift on the surface, even to other females to form strings of argonauts. It is assumed that this is an adaptation to passive, nocturnal hovering on the surface at the time of oviposition and expulsion of the larvae]

NESIS, K. N.

1977. The horizontal and vertical distribution of oceanic cephalopods. 1. S'ezd sov. okeanologov, vyp 2, tezisy dokl. Moscow, Nauka (First session of soviet oceanologists, 2, thesis reports), pp. 126 - 127

[This is a summary of extensive data on the distribution and migration of oceanic cephalopods, especially in boreal and equatorial zones]

NESIS, K. N. & G. A. SHEVTSOV

1977. Neritic squid of the family Loliginidae in the waters of the Soviet Far East. Biol. Morya No. 3, pp. 70 - 71 (ES)

[A juvenile specimen of *Loligo (Doryteuthis) bleekeri* Kefenstein was taken in the South Kurile Strait at 60 - 90 m where apparently it was astray in search of food. This is the first report of this species in Soviet waters]

NIOMATULLIN, CH. M.

1976. The discovery of a gigantic specimen of *Architeuthis* in the equatorial Atlantic Ocean. Biol. Morya, No. 4, pp. 29 - 31 (ES)

[Possible reasons for the anomalous occurrence of *Architeuthis* outside its range are presented]

SHIMANSKY, V. N.

1975. Changes in the cephalopod fauna at the Mesozoic-Cenozoic boundary. MN, Sb. 5, pp. 183 - 185

[At the end of the Mesozoic and the beginning of the Cenozoic, sharp changes are noted in the coleoid and ammonoid cephalopods, while nautiloids altered only slightly. The nautiloids acquired their present day appearance by the end of the Miocene]

STAROBOGATOV, YA. I.

1976. On the homology of the tentacular apparatus of cephalopod mollusks. Evol. Morphol. bespozvonoch. zhivot. (Evol. morphol. of invertebrates), Leningrad, pp. 50 - 51

[It is theorized that the tentacular apparatus of cephalopods is homologous to the lateral tentacles and their placement in the Monoplacophora]

VOVK, A. N., K. N. NESIS & B. G. PANFILOV

1975. The distribution of the deep sea cephalopods in the south Atlantic and adjacent waters. MN, Sb. 5, pp. 162 - 164

[Apparently sperm whales feed on pre-spawning and spawning swarms of cephalopods. Such aggregations usually take place in waters of the continental slope, the submarine heights of the South Atlantic and near the Antarctic convergence]

ZAKHAROV, YU. D. & V. S. KRIVOSHAPKINA

1976. Features of growth and the continuity of shell formation in ammonoids. DVBPI 38 (141): 34 - 71 (ES)

[3 postembryonic stages were observed and a single whorl of the shell was shown to form in 1.3 - 1.7 years]

SCAPHOPODA

CHISTIKOV, S. D.

1975. Some problems of Scaphopod taxonomy. MN, Sb. 5, pp. 18 - 21

[A new system for the order Dentaliida is proposed: Superfamily Quasidentalioida, new (1 family), Superfamily Dentalioida (4 families) and Superfamily Rhabdoidea, new (3 families). Several new familial and subfamilial units are also established]

A. S. Z.

TAMPA MEETING

OF THE AMERICAN SOCIETY OF ZOOLOGISTS
AND SOCIETY OF SYSTEMATIC ZOOLOGY

The American Society of Zoologists and the Society of Systematic Zoology will meet at the Holiday Inn Hotel and Convention Center in Tampa, Florida, December 27 to 30, 1979. Very low room rates are available (\$19.- for single rooms and \$24.- for doubles). The call for contributed papers will be issued in April and the deadline for abstracts is August 31.

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- Physiology of the Avian Egg
- Immunological Memory
- Developmental Biology of Fishes
- Social Signals - Comparative and Endocrine Approaches
- Behavioral and Reproductive Biology of Sea Turtles
- Systematics - Ecology Interface
- Life History Strategies of Marine Organisms
- Applicability of Functional Morphology to the Construction of Classifications and Phylogenies
- Analysis of Form

An all-participant party, a reception and luncheon following the ASZ Presidential Address, and divisional cash bar socials will be arranged. Plans include Commercial Exhibits, a Job Placement Service, and a Babysitting Service.

For more information and abstract forms contact:

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[telephone: (805) 492 4055]

W. S. M.

SYMPOSIUM ON THE LIFE HISTORIES OF MOLLUSKS

Papers on any aspect of molluscan life histories will be considered for presentation at a symposium to be held during the joint meeting of the Western Society of Malacologists and the American Malacological Union in Corpus Christi, Texas, 5 - 11 August 1979. Presentations

should be concerned with an aspect of the reproduction, development, growth, or population dynamics of mollusks. Theoretical papers on the evolution of life history traits of mollusks are also invited. Opportunity for publication of abstracts or full length versions of papers presented at the symposium will be provided. Further information and a 'Call for Papers' is available from:

David R. Lindberg
Center for Coastal Marine Studies
Applied Sciences
University of California, Santa Cruz
Santa Cruz, CA 95064
U. S. A.

ADDITIONAL ERRATA

Dr. Nelson has discovered some more errors in his paper published in our October 1978 issue:

p. 203, column 1, line 4: read "Cenozoic" for "Cenzoic"
Plate figures 6 and 7 (opposite p. 204) should be transposed

p. 207, column 1, Figure 15: the block portion of the right half of the diagram should be black as in Figure 14

p. 210, column 1, Figure 18: the word "upper" should be added to the third block under "Miocene"

These errata are in addition to the 3 corrections made in our January issue, p. 402. Both the Author and the Editor apologize for these errors.

IMPORTANT NOTICE

If the address sheet of this issue is **PINK**, it is to indicate that your dues remittance had not arrived at the time the mailing was prepared (*i. e.*, by March 1, 1979). We wish to take this opportunity to remind our Members that a reinstatement fee of one dollar becomes due if membership renewals have not been received by C. M. S., Inc. by April 15, 1979. However, in view of the unreliability of the postal service, members should not be alarmed by this notice as their remittances may be received between the first of March and the date of mailing this issue on April 1. From overseas addresses we must allow a minimum of 6

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[Part 1: Opisthobranch Mollusks of California
by Prof. Ernst Marcus;

Part 2: The Anaspeida of California by Prof. R. Beeman,
and The Thecosomata and Gymnosomata of the Cali-
fornia Current by Prof. John A. McGowan]

[The two parts are available separately at \$3.- each]

Supplement to Volume 6: out of print.

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ment elsewhere in this issue.

Supplement to Volume 11: \$6.-.

[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Volume 14: \$6.-.

[The Northwest American Tellinidae by Dr. E. V. Coan]

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by WINIFRED H. ARNOLD

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Ovulidae by CRAWFORD NEILL CATE]

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[Growth Rates, Depth Preference and Ecological Succes-
sion of Some Sessile Marine Invertebrates in Monterey
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CALIFORNIA

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is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, the VELIGER. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

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Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15 but before March 15 of the following year, there will be a re-instatement fee of \$1.-. Members whose dues payments (including the re-instatement fee) have not been

received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of \$5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is \$25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

REGARDING POSTAL SERVICE

We are much disturbed by the steadily increasing number of premature claims for supposedly "missing" issues of our journal. Since we have announced on numerous occasions that our journal is mailed on the dates printed in the issues, *i. e.*, number 1 on July 1, number 2 on October 1, number 3 on January 1 and number 4 on April 1 of each volume year, it is unreasonable to expect delivery of the issues earlier than at least one week after these dates; however, a much longer time must be allowed for delivery to addresses at various distances from Berkeley. Thus, for example, a two weeks lapse is not unusual for as short distances as 500km; and up to 3 and 4 months must be counted on for addresses in the Far East and in Africa. We are faced with the alternative of not replying to what we must consider premature claims or, if the trend continues, we must increase our subscription rates to cover these additional expenses. Our past efforts at keeping the subscription rate as low as possible are, we believe, sufficient evidence that we simply cannot afford any other course of action. The postal service causes us enough financial losses. Therefore we urgently request that before

a claim is made, the time schedule be carefully checked. We are grateful for the understanding of this difficult situation shown by many librarians and will be grateful to those who, heretofore being perhaps eager to make sure that the library receives what is coming to it, will exercise a little patience.

Your harassed Editor.

The Latest New Postage Rates

Effective on May 29, 1978, the U. S. Postal Service increased rates for first, third and fourth class matter, as announced some months before. However, although not announced publicly and without notification to publishers, second class postage rates within the United States were also increased. Further, again without advance notification, postage for second class matter to the so-called PU-AS countries (Spanish-speaking countries and Brasil), which had traditionally been lower than to all other foreign countries, was increased to the same rate.

On July 6 a further increase of postage rates within the United States went into effect. This increase came also as a surprise to us, since we had assumed that the May increase was taking the place of the so-called phased increases which are scheduled for the sixth of July each year.

It is obvious that we are forced to pass these increases on to our members and subscribers. Therefore, effective immediately, we must charge US\$3.50 for postage to all addresses outside the United States, and \$1.50 for all domestic addresses.

Under no circumstances are we able to supply free replacement copies of issues that fail to reach their proper destination. However, we will ship by insured mail replacement copies at half the announced single copy rate of the particular issue plus postage. We have developed a triple check system so that, if we say that a copy has been mailed, we are absolutely certain that we delivered that copy to the post office in Berkeley and on the date we indicate. From our experience with the loss of insured mail, we are tempted to suggest that subscribers figure on a 10% reserve fund for the purchase of replacement copies. The only alternative remaining would be for us to increase subscription rates and membership dues by at least 10%. This, however, does not seem quite fair to us as some of our subscribers in almost 20 years have never failed to receive their copies.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time, that is 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed \$400.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, \$400.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U. S. A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are sub-

mitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript – including figure explanations and the “Literature Cited” section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the “dead letter” office, in other words, it is destroyed.

BOOKS, PERIODICALS, PAMPHLETS

The North Pacific Cretaceous Trigoniid Genus *Yaadia*

by LOUELLA R. SAUL. Univ. Calif. Publ. Geol. Sci. 119: 1 - 65; 12 pls. \$7.25 (30 June 1978)

Although first glance at the title and contents suggest another detailed taxonomic and nomenclatural revisionary monograph, careful examination reveals a more broadly comprehensive and detailed study of the highly ornamented “knobby trigoniids,” an extinct group of highly successful (abundant and diverse) predominantly Cretaceous bivalves. In addition to taxonomic treatment of the North Pacific species, the author provides us with a review of the world-wide occurrence of the 4 major genera of knobby trigoniids through the Cretaceous stages.

Attempts to fit paleontological data to recent ecological and evolutionary theory are often less than successful, and

the author's allusion to *r*- and *K*-strategies (p. 23) is far removed from the original mathematical context of a theory that has been rather thoroughly shot full of holes by ecologists and evolutionary biologists. Paleontologists would do well likewise to abandon a theory that has even less meaning within the context of the fossil record. But this is a minor quarrel.

I was most interested in the author's analysis of trigoniid functional morphology, because it follows closely upon the publication of STANLEY's (1977) analysis of the functional morphology of the same group. It is curious that neither author seems to have been aware of the other's work. It is even more curious that the results are so different. Without interjecting my own predilections at this point, I suggest that anyone interested in bivalve functional morphology examine and compare the basic assumptions, observational data, and conclusions of Saul and Stanley. Even given a basic agreement about the locations of inhalent and exhalent currents and the foot, they have positioned their animals differently with respect to the sediment-water interface and arrive at very different conclusions with respect to the adaptive significance of the discordant sculpture in trigoniids, both with respect to its possible function as an aid in burrowing and its hydrodynamic effects. I would further suggest that the results of critical comparison may not lead the reader simply to taking the side of one author exclusively against the other without asking some critical questions of both.

Whatever conclusions the reader reaches with respect to the ecological and evolutionary interpretations, this publication provides an exceptionally comprehensive and useful taxonomic, paleogeographic, and biostratigraphic analysis of a group of fossil bivalves that has been heretofore very poorly understood. It should also serve to stimulate further interest in the Trigoniidae.

Carole S. Hickman
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Literature Cited

- STANLEY, S. M.
1977. Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. *Paleontology* 20 (4): 869 - 899 (December 1977)

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in **THE VELIGER** is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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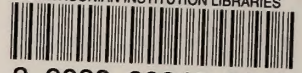
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